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Fahy, W. E. and O'Hara, R. K. Does salinity influence the number of vertebrae developing in fishes? J. Cons. int. Explor. Mer, 37: 156–61.

Page 156. Under Materials and methods, line 11, delete 100; to read (one I.U./g body ...)

Page 157. Under Results, right-hand column at bottom of first paragraph, 0·596; to read 1·68.

Page 157. Bottom line of Table 2, the numerator and denominator in the Equation for F should be interchanged and the correct value for F inserted; to read

$$F = \frac{0{\cdot}441}{0{\cdot}263} = 1{\cdot}68$$

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Field tests of seabed drifters, using sector-scanning sonar techniques

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Woodhead seabed drifters equipped with acoustic transponding tags were tracked by sector scanning sonar in four separate exercises off the Suffolk coast (Southern North Sea). Remote measurements of the height of each drifter relative to the sea bed were made at 5 min intervals over at least one tide, and these observations were related to measurements of *midwater* current velocity obtained at sites close to the drifters' paths. These results show that the drifters remain on the sea bed until the midwater current exceeds 50 cm s^{-1} (approximately). Thereafter, at midwater current velocities of 50–95 cm s^{-1} saltation occurs at an increasing frequency though the drifter tends to remain within 3·5 m of the sea bed. At midwater current velocities greater than 95 cm s^{-1} the drifter lifts from the near-bottom layer to glide for extended periods of time in midwater.

Introduction

nce its first use in the early 1960s, the Woodhead abed drifter has gained widespread acceptance as a eap indicator of near-bottom residual water-move- ents in the shallow waters of the continental shelf; e results obtained by its use have been applied to e dispersion of radioactive and other pollutants, e behaviour and movements of shrimp and young h, the movement of sediments and other related oblems.

The development of the seabed drifter has been scribed by Woodhead and Lee (1960) and by e, Bumpus and Lauzier (1965). In its standard rm, the drifter consists of a buoyant polyethylene p and stem, with a copper weight crimped to the se of the stem in order to provide a slight net gative buoyancy. In use, the inherent imprecision the technique demands that the drifters are re- ased in quantity at each station, and at the Lowes- ft Laboratory little attention is given to stations at ich less than 40% of drifters are returned within weeks of release since this would otherwise place due importance on the returns of a few individual ifters. Recoveries are made by fishing vessels or m beaches, and different sea-areas may show arked differences in the percentage recovered from ch source (Ramster, 1965).

While the influence of human, tidal and wind ctors on drifter returns has received considerable tention (summarised in Riley and Ramster, 1972), the performance of drifters at different rates of water-flow is less well understood. Indeed the limitations imposed by the size and velocity-range of flumes and the restrictions on diver inspection at sea have meant that our ideas of drifter behaviour at sea are based on relatively low-speed flume tests together with indications of drifter behaviour inferred from the working-up of anomalous drifter returns.

The two aspects of drifter performance that may be expected to have the greatest bearing on the accuracy of bottom drift estimates are the match of drifter speed to water speed, and the ability of the drifter to keep within the near-bottom layer. Although this paper is principally concerned with the latter aspect of performance, the former subject must also be discussed here since both are functions of the weighting (≈ depth-stability) of drifters, and since some confusion appears to have arisen in the literature concerning the match of drifter and water speeds.

Flume tests

The performance characteristics of seabed drifters were first examined by the Lowestoft Laboratory in two series of flume tests. In the first series an early pattern of drifter was used which was dissimilar in design, in unballasted buoyancy and in the variability of unballasted buoyancy from the standard drifter in production today. As a result the performance figures quoted by Woodhead and Lee (1960) are not applicable to drifters now in use (cf. Morse, Gross and Barnes, 1968, p. 101).

A second series of flume tests using drifters of the modern type was carried out in 1961 by D. J. Ellett of the Lowestoft Laboratory (1962, unpublished internal report). Forty-seven drifters having a mean weight in fresh water of 1·65 g were timed along a 5 or $2\frac{1}{2}$ metre length of flume at seven water speeds between 7·7 and 48 cm sec^{-1} (cf. Ramster, 1965; Philips, 1970). The results of 10 runs were rejected and the mean regression of water velocity on drifter velocity for the remaining 319 runs was

$$y = 1{\cdot}099x + 3{\cdot}90$$

where y is the water speed, x the drifter speed and the units are cm sec^{-1}. (A single drifter was timed along ten replicate runs at each of 5 water speeds between 7·7 and 44·0 cm sec^{-1} to test the reproducibility of results). From these results (Figure 1) it is evident that at water speeds between 20 and 50 cm sec^{-1} the drifters behaved well. Strictly these results apply to a drifter with a net negative buoyancy of 1·65 g, though by analogy with other tests of pre-production drifters at different weightings, Ellett suggests that these results may be applied without serious error to the standard production drifters used by the Lowestoft Laboratory which are calculated to have a net weight of 1 g in sea water.

From Figure 1 the threshold water speed for drifter movement is satisfactorily low. This is important since, as Ramster (1965) points out, a higher threshold speed might seriously bias our estimates of residual drift. If for example, tidal flood streams attain faster speeds than those of the ebb, this could mean, that during the slacker ebb phases of each tide, the water is moving slowly past the drifter without transporting it, so that the final pattern of drifter returns is merely a reflection of the stronger flood currents and not of the true residual drift. Under these circumstances the drifter may even indicate a residual flow where no net water transport takes place. However, since we normally know little more of the drifter's track than may be inferred from the positions and dates of release and recovery, the threshold values obtained in flumes have remained untested in the changing conditions of tide, wave, velocity-shear and bottom topography that form the environment of the drifter at sea.

Once the threshold water-speed for drifter movement is exceeded to the point where artificial tidal "selection" can no longer apply, then the mismatch between drifter and water speeds becomes progressively less important as a source of error in estimating residual bottom drift. The expected (and unknown) time-lag between the date of stranding and the date of recovery reduces the significance of any sligh delay in the arrival of the drifter on the beach. Above a certain value of current speed however, a second more important source of error could arise. If th increasing turbulence is able to lift the drifter from the sea bed for prolonged periods, it is clear that the track taken by the drifter could be seriously in error especially if the drifter is "sampling" different part of a two-layer or multi-layer circulation at differen phases of the tide. The slight weighting of the drifte in sea water (together with the effect of the cap perforations) was designed to resist this tendency, ye no greater weighting could be used without impairin either the low-speed performance of the drifter or it essential ability to lift easily over obstacles in its path

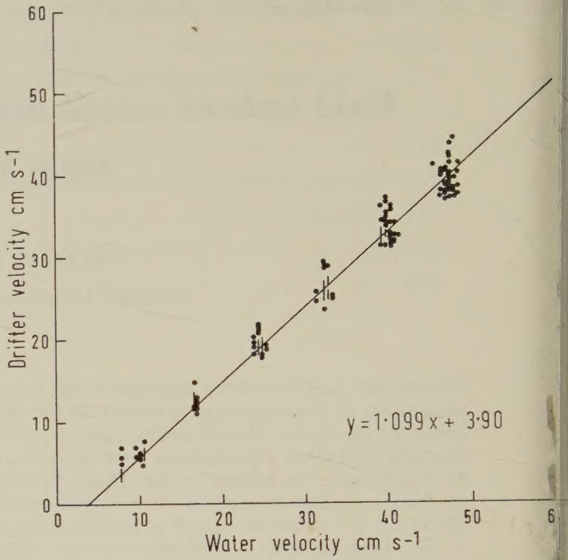
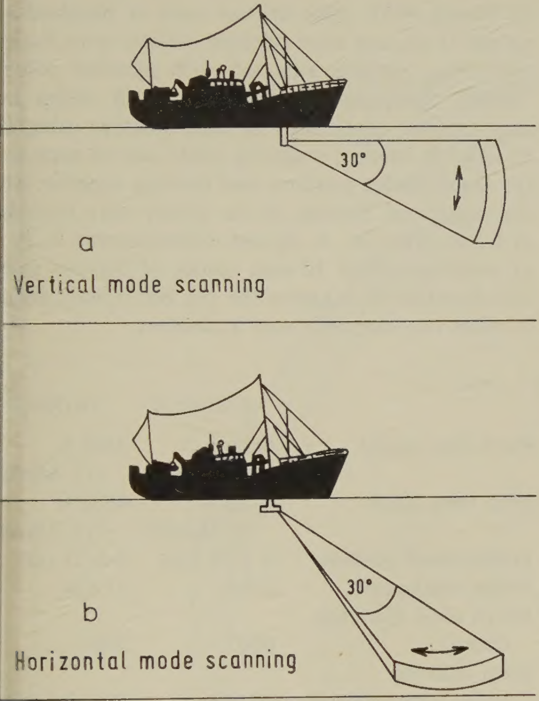


Figure 1. Regression of drifter speed on water speed fo standard production drifters (from Ellett 1962).

Early field tests using sonar

Recently, the miniaturisation of sonar transmitter and transponders has for the first time permitte the study of drifter behaviour at sea.

Folger (1971) reports the tracking of eight drifter equipped with sonar transmitters in Somes Bay Maine and in Massachusetts Bay; hydrophones wer used to locate each drifter at irregular intervals (onc or twice per day). From the point of view of th present discussion it is unfortunate that no simultaneous current meter observations were made as check on the drifters' performance and (perhaps c less significance) that the syntactic foam block whic was added to neutralise the weight of the transmitte



igure 2. Diagrammatic view of Scanner beam in (a) ertical mode scanning and (b) Horizontal mode anning.

as located just below the cap so as to block the four p perforations.

More recently the installation of an advanced high solution sector-scanning sonar system aboard RV lione' and the development of a small transpondg fish tag have enabled staff of the Lowestoft Laborory to carry out more detailed studies of drifter rformance at sea.

The ARL scanning sonar system has been deribed by Voglis and Cook (1966) and Mitson and ook (1971). It operates at a frequency of 300 kHz d scans a 30° sector at a rate of 10 000 sweeps r second. The transducer can be steered manually azimuth through 360° and tilted through 90° thus lowing the operator to inspect any 30° sector of a bed or water column around the ship. The rerned signals are displayed on a B-scan cathode ray be to give a pictorial representation of the seabed in to a television display. The basic usefulness of e system lies in the high resolution of the acoustic splay (7 cm in range; ¼° in bearing) and in the ct that two scanning modes are possible. When e transducer is horizontally aligned the 30° sector scanned laterally (Fig. 2b) and the display prents a more or less inclined "birds-eye view" of the sea bed; when the transducer is aligned vertically (Fig. 2a) a narrow vertical section from sea-surface to sea bed is scanned and displayed. Accordingly, by tracking an acoustically-tagged drifter in vertical mode, the height of the drifter above the sea bed may be monitored continuously. When the drifter is seen to lift from the sea bed accurate remote measurements of drifter height may be made by tilting the transducer until first the tag signal and then the sea bed beneath it are brought onto the centre line of the display (representing the centre of the main scanner beam). Since the tilt angle of the centre of the beam is shown digitally on the display, the height of the drifter (H) is found by

$$H = \text{range}\ \sin\theta' - \text{range}\ \sin\theta$$

where "range" is the slant range from the transducer to the target, and θ and θ' are the tilt angles required to bring the tag signal and the underlying sea bed onto the centre line of the display (respectively). The accuracy of this remote measurement technique has been tested by Dickson and Lee (1973) in that scanner estimates of the depth of dredged pits on the seafloor were compared with direct measurements by divers. At 90–120 m range the difference between the remote and direct measurements of pit depth was found to be less than 0·1 m. Some lesser accuracy is to be expected in the measurements of drifter height described below since, in contrast to the experiments just described, neither the ship nor the target was stationary, but their relative motion was sufficiently slow to prevent a serious increase in error.

The acoustic transponding tag with which the drifters were equipped has been described by Mitson and Storeton-West (1971). Briefly, its activity is as follows. In short range operation the scanner transmits four times per second. On receipt of the 100 μs pulse transmitted by the scanner, a 3 ms return pulse is transmitted by the tag. The tag then blanks out for 25 ms to allow reverberations of the scanner pulse and of its own return pulse to fade. This minimises the spurious interrogation of the tag by signals reflected from the sea surface, sea bed and ship.

Using this system, Harden Jones, Greer Walker and Arnold (1973) were able to track a tagged drifter for 25 h, noting the position of the ship, the range and bearing of the drifter and the drifter's height above the sea bed at 15 min intervals. A parachute drogue was subsequently tracked at midwater depth to establish the strength of tide at half hourly intervals. From this exercise they were able to demonstrate that the drifter was lifted clear of the bottom during the strongest part of the tide, initially in a series of hops, but later in a sustained midwater "glide" of up to 15 min duration at peak tide. These observations were made during the course of a fish-tracking cruise. Unfortunately because there was at the time no method of accurately weighting the modified drifter, the observations inevitably suffer from the limitation that the net weight of the drifter in sea water was unknown, beyond the fact that the drifter carried sufficient weight to sink to the bottom on release. The series of tests reported below was therefore designed to test the reproducibility of these preliminary results.

Recent sector-scanner studies

By accurately weighing each drifter component in sea water (salinity 33·866‰ σ_t + 26·087) four drifters were made up for sea tests as shown in Table 1.

Table 1. Net buoyancy of seabed drifters used in field tests

Drifter	Buoyancy in sea water (grams)			
	Stem + cap	Acoustic tag	Copper wire ballast	Assembled drifter
C	+5·49	−3·40	−4·09	−2
H	+5·52	−3·38	−3·14	−1
I	+5·53	−3·38	−3·15	−1
J	+5·67	−3·43	−3·24	−1

These drifters were then tracked over at least one complete tide as described below and the performance of each was compared with water movements recorded using a Plessey M.O.21 self-recording current meter, moored close to the anticipated path of the drifter. It should be noted that water movements were monitored *at midwater depth* throughout these experiments, partly because of the difficulty of mooring current meters in the near-bottom boundary layer, but also in order that other users of seabed drifters might be able to relate the results obtained to the specific conditions of current strength obtaining in their area; it was thought likely that midwater current strength would be a more generally-known parameter than the current shear within one meter of the sea bed.

Drifters H and I (1 g)
Southwold–Thorpeness Area

Two tracking exercises were carried out off the Suffolk coast (southwestern North Sea) on 9 and 11 March 1973. Both drifters were of standard ne weight (1 g), and were released directly onto the sea bed using weights attached with seawater soluble "string" (polyvinyl alcohol film). Each drifter was then tracked continually in calm weather using the Scanner in vertical scanning mode and in each case the ship's Decca position and heading together with the range and bearing of the drifter were recorded at 5 min intervals. A current meter moored in 19 m of water provided 10 min values of current speed and direction 9 m above the sea bed. Other details of these two exercises were as follows:

	Drifter H	Drifter I
Start time (date)	0850 h (9 March)	2105 h (11 March)
Stop time (date)	1715 h (9 March)	0330 h (12 March)
Duration of tracking	8 h 25 min	6 h 25 min
Mean windspeed	7 kts	11 kts
Mean wind direction (from)	024°	358°
Data interval (wind observations)	60 min	60 min
Sounding	16–18 m	19–21 m
Data interval (soundings)	5 min	5 min

Figure 3 shows the track of each drifter (from 5 minute fixes) during separate south-going tides with progressive vector diagrams at the same geographical scale (from 10 min values) representing the water movements at the position of the current meter mooring.

Drifters J (1 g) and C (2 g)
Shipwash area

Two further experiments, one using a drifter c standard weight and another of double the standar weight were conducted in the vicinity of the Shipwash Lightvessel on 17 and 18 March 1973. The drifter were tracked in calm weather over a south-going and a north-going tide (respectively); as in the case of drifters H and I, the location of the drifters wa determined at 5 min intervals while a current mete mooring in 19 m of water provided 10 min value of current speed and direction at midwater dept (9 m above the sea bed). Multiple soundings alon the path of the drifters showed a markedly greate and more variable water depth than in the case c

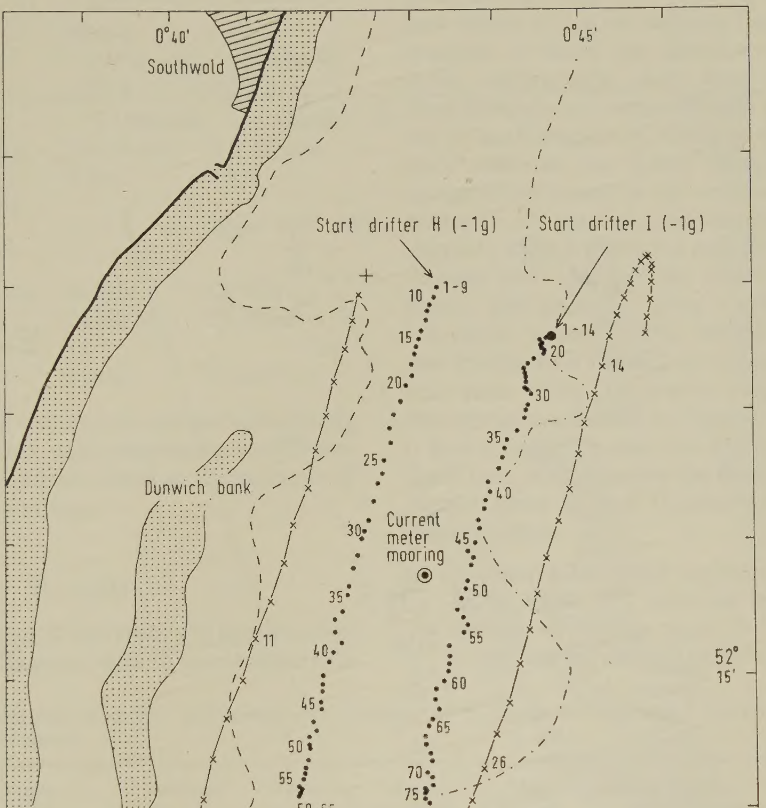

0°40'
Southwold
0°45'
Start drifter H (-1g)
Start drifter I (-1g)
1-9
10
15
20
25
30
35
40
45
50
55
59-65
1-14
20
30
35
40
45
50
55
60
65
70
75
78
14
26
39
11
22
Current meter mooring
Dunwich bank
Sizewell bank
2·5 fm
2·5 fm
6 fm
10 fm
52° 15'
0
1
2
3
4
5
Kilometres

Figure 3. Track of drifters H and I together with progressive vector diagrams at the same geographical scale representing the midwater flow through the position of current meter mooring. The position of each drifter was determined at five-minute intervals (dots) and these fixes are numbered along each drifter's track. The progressive vector diagrams (crosses) are constructed from measurements of the current at ten-minute intervals.

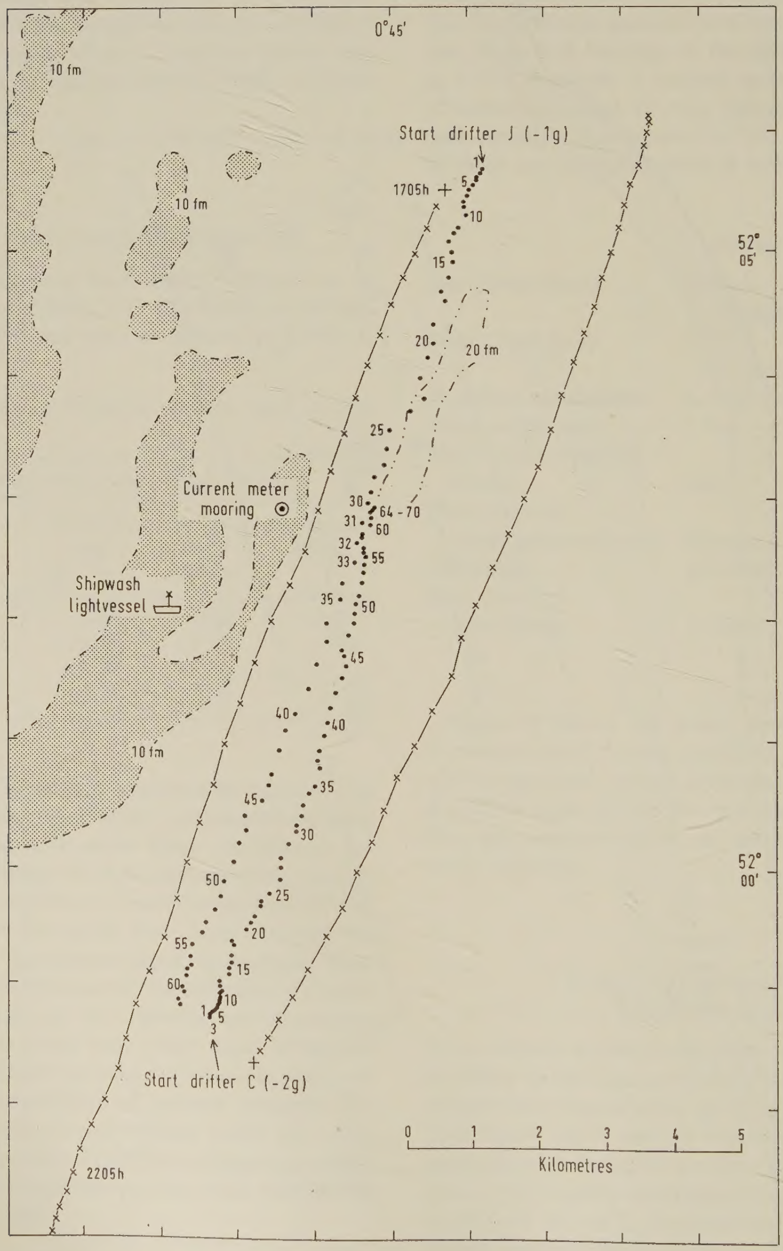

0°45'
10 fm
10 fm
10 fm
20 fm
Start drifter J (-1g)
1705h
Current meter mooring
Shipwash lightvessel
Start drifter C (-2g)
2205h
52° 05'
52° 00'
0 1 2 3 4 5
Kilometres

Figure 4. Track of drifters J and C together with progressive vector diagrams at the same geographical scale representing the midwater flow through the position of current meter mooring. The position of each drifter was determined at five-minute intervals (dots) and these fixes are numbered along each drifter's track. The progressive vector diagrams (crosses) are constructed from measurements of the current at ten-minute intervals.

e earlier exercises just described. Other details are . follows:

	Drifter J	Drifter C
art time (date)	1705 h (17 March)	1130 h (18 March)
op time (date)	2215 h (17 March)	1715 h (18 March)
uration of tracking	5 h 10 min	5 h 45 min
ean windspeed	0 kts	7 kts
ean wind direction (from)	–	353°
ata interval (wind observations)	60 min	60 min
ounding	24–40 m	25–38 m
ata interval (soundings)	5 min	5 min

As before, Figure 4 shows the track of each drifter min fixes) together with progressive vector dia-ams of midwater current speed at the position of e current meter mooring.

Results

Figures 3 and 4 each drifter track and its associated ogressive vector diagram refer to identical periods of time and permit a detailed comparison between drifter speed and midwater current speed over any given period of the tide. In Table 2 the results from each drifter of 1 g net negative buoyancy have been analysed to show the distance covered by each drifter during each whole hour of tracking, and these distances are compared with the corresponding water "path-length" at midwater depth. (In the two cases indicated the drifter appears to have been temporarily trapped by the weight used to carry the drifter to the sea bed, and these results have been ignored.) Drifter H was the only drifter to be tracked through two tides and the intervening slack water period, and since this gives a valuable measure of "threshold velocity", the drifter's performance is also analysed for the half-hourly periods before and after slack water. The results listed in Table 2 are also shown graphically in Figure 5.

In this figure the mean hourly speeds of drifters H, I and J are plotted against the mean hourly midwater current speed at each location and it would seem from this that:

(i) A linear relationship appears to exist between drifter speed and midwater current speed over the current velocity range 10–95 cm sec^{-1}. Since in this case the drifter's performance (presumably

able 2. Hourly estimates of drifter performance in relation to midwater current speed for all drifters of 1 g net negative buoyancy

Drifter	Time GMT	Drifter movement (km)	Water movement (km)	Mean drifter speed (cm sec^{-1})	Mean water speed (cm sec^{-1})	Drifter speed as a % of water speed	Remarks
H	0850–0950	0·48	2·53	12·7	70·3	19·0*	Ignored, Drifter trapped by release weight?
	0950–1050	2·07	3·36	57·6	93·4	61·7	
	1050–1150	2·33	3·38	64·7	93·9	68·8	
	1150–1250	1·68	2·85	46·7	79·1	59·0	
	1250–1350	0·89	1·74	24·8	48·5	51·2	
	1350–1450	0·27	0·78	7·7	21·7	35·6	
	(1350–1420)	0·04	0·23	2·1	13·0	16·1	Half-hourly estimates of drifter and water movement
	(1420–1450)	0·24	0·57	13·6	31·7	42·1	
	1450–1550	1·28	2·67	35·7	74·2	48·1	
	1550–1650	2·19	3·36	60·9	93·3	65·2	
I	2105–2205	0	1·08	0	30·0	0 *	Ignored
	2205–2305	0·58	0·97	16·1	26·9	59·6	
	2305–0005	1·24	2·54	34·6	70·6	49·0	
	0005–0105	1·78	3·11	49·6	86·4	57·3	
	0105–0205	1·58	2·81	43·8	78·1	56·0	
	0205–0305	1·41	2·28	39·2	63·3	61·8	
J	1705–1805	1·21	2·46	33·5	68·3	49·2	
	1805–1905	2·99	3·50	83·0	97·2	85·4	
	1905–2005	3·35	3·84	93·0	106·7	87·2	
	2005–2105	3·60	3·63	99·9	100·8	99·2	
	2105–2205	2·11	2·82	58·5	78·3	74·8	

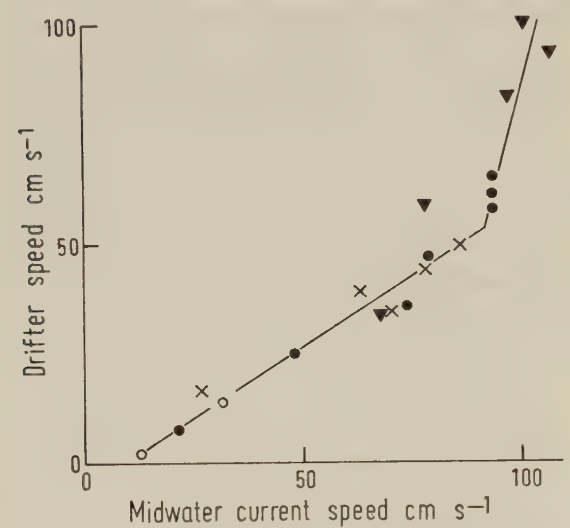


Figure 5. Comparison of observed drifter speed to midwater current speed during each whole hour of tracking (drifters H, I and J). Key to symbols: Drifter H ●, (half-hourly estimates shown as open circles), Drifter I ×, Drifter J ▼.

in the near-bottom boundary layer) is compared with *midwater* current estimates, the slope of the regression is shallower than that shown in Figure 1.

(ii) This linear relationship indicates that threshold drifter movement takes place when the *midwater* current velocity reaches approximately 10 cm sec^{-1}. (Again, due to the expected velocity shear between midwater depth and the seabed the actual threshold velocity affecting the drifter in the boundary layer is likely to be somewhat less than 10 cm sec^{-1} in apparent confirmation of the results obtained in flume tests).

(iii) At midwater current speeds greater than 90–95 cm sec^{-1}, the slope of the regression between drifter speed and water speed becomes very much steeper. The drifter's "stability threshold" has evidently been exceeded by intense turbulence and the drifter has been lifted clear of the sea bed to glide for prolonged periods in the midwater flow.

(iv) Despite the fact that the individual tracking exercises took place over a range of depths from 16–40 m, the results from all three drifters seem compatible.

During the tracking of drifters H, I, J and C the drifter's height relative to the sea bed was continuously monitored using the scanner in vertical mode. Discrete quantitative height estimates were made at 5 min intervals and at the peak of each major excursion from the sea bed by means of the technique described above (p. 5). Since this technique

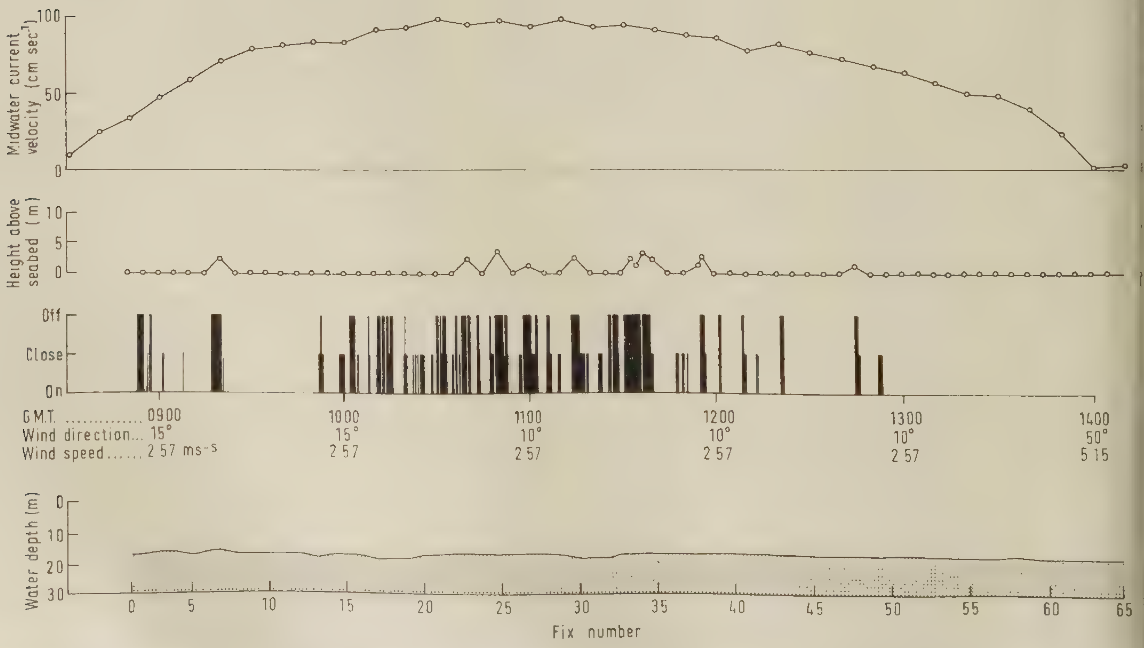
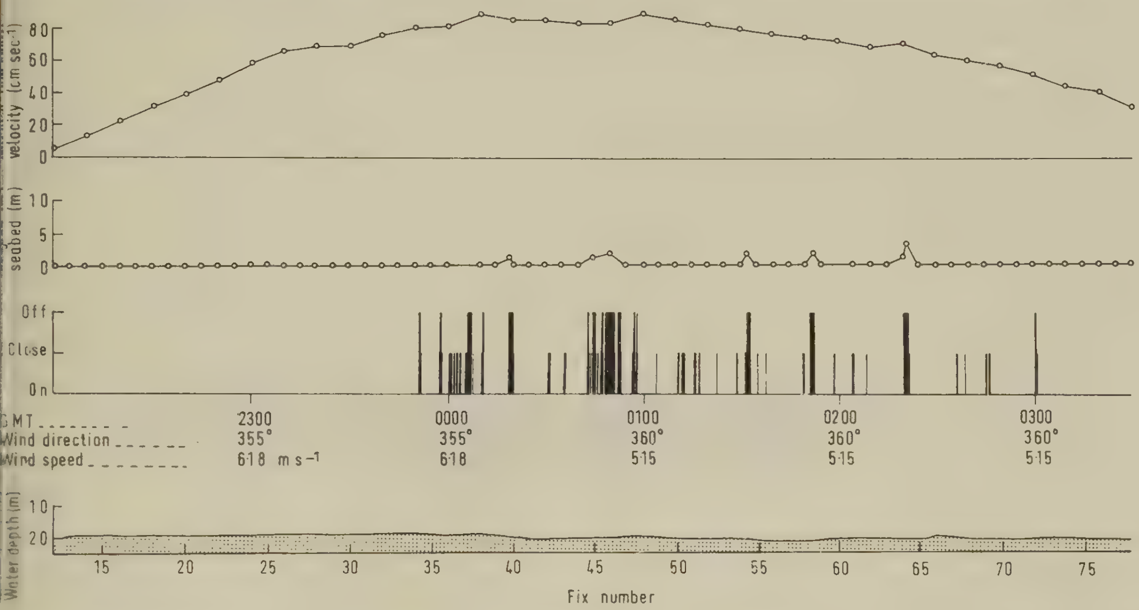


Figure 6. Composite plot of all data relevant to tracking of drifter H. The fix numbers refer to the positions of the drifter at five-minute intervals (see Figure 3).



igure 7. Composite plot of all data relevant to tracking of drifter I. The fix numbers refer to the positions of the ifter at five-minute intervals (see Figure 3).

volves precise changes in the tilt of the scanner ansducer, these estimates could not be made with fficient speed to describe each minor excursion om the bottom, and this rapid "saltation" was corded qualitatively using the following method. he height of the drifter relative to the sea bed was assified according to three categories.

) "On the bottom". Tag signal merged with sea bed.

i) "Close to the bottom". Tag signal proud of the sea bed but contiguous with it.

ii) "Off the bottom". Tag signal clearly separated from the bottom. This category was used to describe all cases when the drifter was clear of the sea bed irrespective of whether the drifter was just clear of the bottom or at midwater depth.

sing a simple rotary "switch" connected to an alogue recorder the scanner operator continuously corded each change in height according to these ree categories, while an event marker was used to nnotate the trace at 1 minute intervals. Figures 6, and 8 represent the detailed activity of drifters H, and J respectively. Each figure shows 10 min values midwater current speed in relation to the drifter's eight above the sea bed. These are given both as screte quantitative estimates at 5 min intervals and as continuous categorised estimates. Five minute values of water depth are also shown and each parameter is plotted versus time for one complete tide. The "fix numbers" shown represent successive determinations of the drifters' position and permit these graphs to be related to the track charts shown in Figures 3 and 4.

The detailed records of Figures 6–8 confirm the basic features of drifter behaviour which were inferred from Figure 5. Notably they confirm that the transition between saltation and prolonged lift-off occurs over a rather narrow range of (midwater) current velocities between 90 and 100 cm sec^{-1}. However the graphs also provide additional information regarding the precise duration of lift-off and the maximum height attained.

Drifter I (Fig. 6), behaved well and showed no tendency to move through the saltation phase into the phase of prolonged lift-off. The drifter was clear of the sea bed for a maximum of 3 min during peak tide (83–88 cm sec^{-1} at midwater depth; fix 46 approx) and never rose higher than 3·5 m from the sea bed in a water depth of 20 m.

Drifter H (Fig. 7) was subject to slightly stronger currents, but again behaved well, showing only the beginnings of a tendency towards prolonged lift-off at peak tide. The most sustained excursion lasted

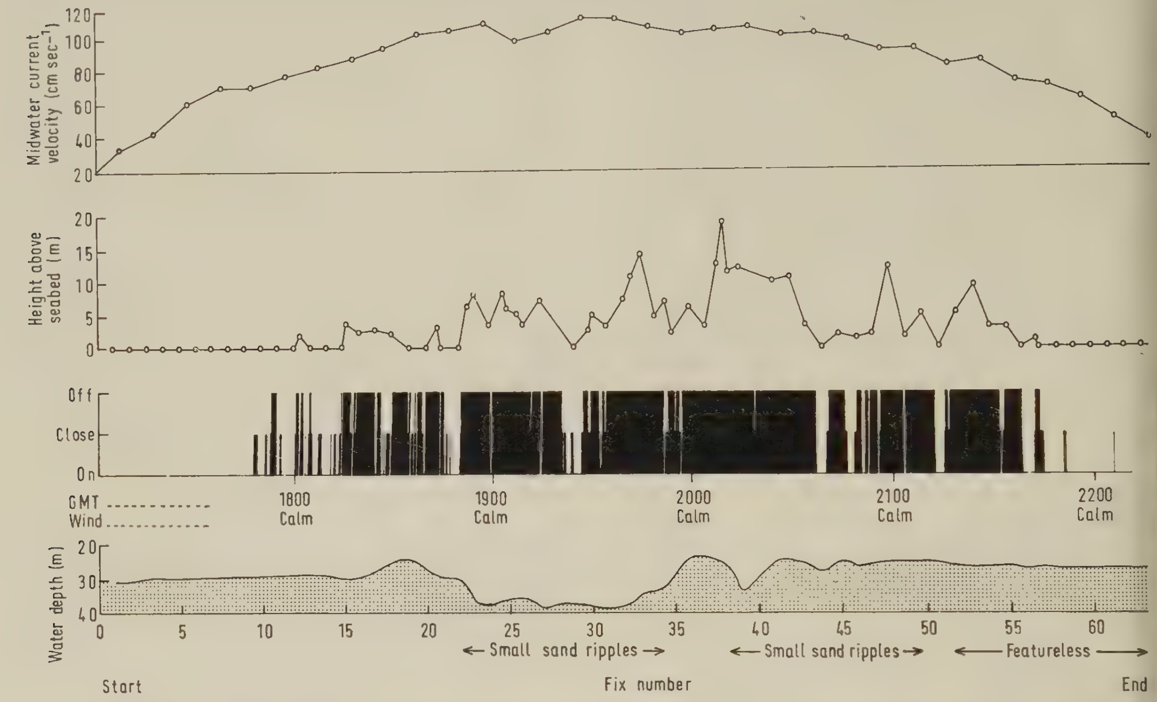


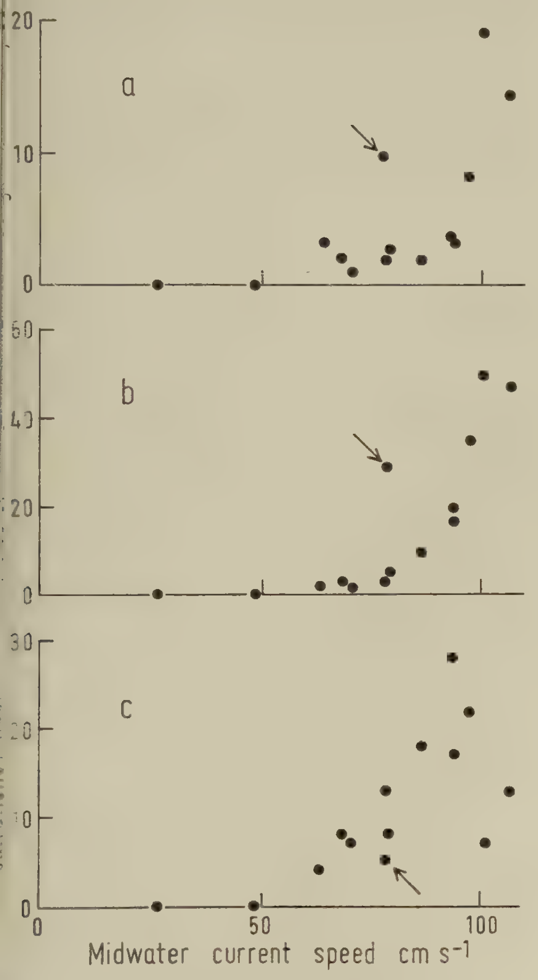
Figure 8. Composite plot of all data relevant to tracking of drifter J. The fix numbers refer to the positions of the drifter at five-minute intervals (see Figure 4).

5½ min during a period when the drifter was clear of the bottom for a total of 8 min out of 8½ min. (The midwater current velocity at this time was 94 cm sec^{-1}; fixes 33–35 approx). During the whole period of observation however, the drifter never rose higher than 4 m from the seabed in 17 m water-depth.

Drifter J (Fig. 8) presents a very different pattern of behaviour. In this case the midwater current reached speeds of 100–112 cm sec^{-1} at peak tide and during this period the normal saltation of the drifter was replaced by prolonged gliding in the midwater stream. Over one period of 63 min (fixes 30–44 approx) the drifter was clear of the bottom for a total of 59 minutes (up to 21½ minutes continuously), "close to the bottom" for 3½ minutes and "on the bottom" for about ½ minute. At this time the midwater current averaged 106 cm sec^{-1} and the drifter was certainly travelling well within the midwater flow, reaching a peak height of 19 m above the sea bed in 26 m water-depth. Although the bottom topography was irregular over this part of the drifter's track the major excursions from the sea bed do not seem to be related either to the main breaks of slope or to the presence of sand waves.

The detailed information contained in Figures 6–8 is summarised more conveniently in Figure 9. The hours over which each parameter is summarised are those listed in Table 2. The results obtained in one particular hour during the tracking of drifter J appear to be anomalous and these values are indicated by arrows. (In this particular case, the drifter's speed appears to be higher than would be expected from the midwater current speed and may indicate that the tide slackened earlier at midwater depth than in the near-bottom layer).

One significant result is found by comparing the maximum height attained by the drifter (Fig. 9a) with the number of minutes per hour spent clear of the bottom (Fig. 9b). This shows that although the time spent off the bottom begins to increase as soon as the midwater current attains a velocity of 80 cm sec^{-1}, the actual height attained does not increase significantly until the midwater flow strengthens to about 95 cm sec^{-1}. At (midwater) current speeds of 80 to 95 cm sec^{-1} the drifter increases its frequency of saltation but tends to remain within 3½ metres of the sea bed. In Figure 9c it is apparent that no saltation takes place until the midwater current has strengthened to 50 cm sec^{-1} (approximately). Thereafter the saltation frequency increases steadily until it reaches a maximum at a midwater current velocity of around 95 cm sec^{-1}



gure 9. Drifter performance in relation to midwater rrent speed during each whole hour of tracking ifters H, I and J). For arrowed point, see text.

Maximum height above sea bed
Total duration of all excursions from the sea bed
Total number of saltations.

higher current speeds, the drifter enters the phase prolonged lift-off making fewer but longer excur- rs from the sea bed, and the saltation frequency eases abruptly as a result.

As mentioned earlier, there were both theoretical d practical reasons for relating drifter performance *midwater* current speed throughout these tests. e main practical reason stemmed from the diffi- ty of making remote and detailed measurements the near-bottom velocity profile while the drifters re being tracked from a moving ship. However ring a subsequent cruise in January 1975, near- ttom current measurements were obtained from the location where the midwater current had been monitored during the tracking of drifters H and I (see Fig. 3). These measurements were obtained using a shear velocity current meter consisting of five S-rotors suspended from a heavy tetrapod frame at heights of 28, 48, 72, 102 and 152 cm above the bed. A direct reading current meter suspended (as before) at a height of 9 m above the bed and coupled to an analogue recorder provided simultaneous measurements of the midwater flow. While these later observations cannot exactly duplicate the conditions of wind and tide obtaining in the original tracking exercise, they do refer to the south going flow at spring tides (as before) and to light winds (9–12 knots, 210°T as compared with 7–11 knots 358°T in the original experiment). Thus it is thought that the results give some indication of the near bottom velocities that obtained during the tracking of drifters H and I. Figure 10 shows the 5-min mean values of midwater and near-bottom current speed that were observed as the tide reached maximum strength. Since the midwater current attained a maximum 5-min mean value of 90·5 cm sec^{-1} this corresponds to the period just before lift-off when the drifter would be in the phase of rapid saltation within 3·5 m of the sea bed. It would clearly be unwise to "over-interpret" these later results but, by extrapolation, Figure 10 would appear to suggest that as the midwater flow strengthens from 90–95 cm sec^{-1} and as the drifter moves through the saltation phase to-

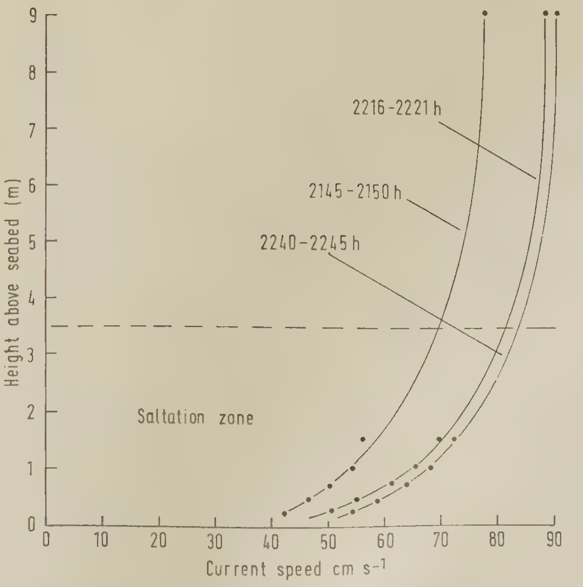


Figure 10. Velocity profiles observed at peak flood tide (south going) at 52°15·7′N 01°43·2′E, 2 January 1975. (5 min mean values).

wards the phase of prolonged lift-off, the currents to which it is subjected are only slightly lower than those at midwater (68–75 cm sec^{-1} at a height of 1 m, but 85–90 cm sec^{-1} at its maximum saltation height of 3·5 m above the bed).

Thus far no reference has been made to the performance of drifter C. This drifter was ballasted at twice the normal net weight in order to find out whether this would improve the depth-keeping properties of the drifter at high current speeds without impairing its low velocity performance. (The track of the drifter together with the progressive vector diagram of the relevant midwater currents are shown in Figure 4). The results obtained were inconclusive. Although the midwater current reached a maximum speed of 100 cm sec^{-1} this was an isolated value and speeds of around 95 cm sec^{-1} at peak tide were more general. Thus the current lay at, but not above, the established threshold value for prolonged lift-off and the results can give no indication as to whether this threshold may be raised by increasing the drifters weight. Over the lower part of the velocity range, the drifter's behaviour appeared to be rather more erratic than was the case with the standard drifters.

Discussion

These experiments, though limited in number, do confirm the observation of Harden Jones et al. (1973) that under certain circumstances seabed drifters may lift from the near-bottom layer to glide for extended periods in the upper part of the water column. Specifically this lift-off appears to occur at a midwater current speed of around 2 kts. Quite clearly this type of behaviour will lead to some misrepresentation of the near-bottom flow patterns (speed and/or direction), wherever these tidal conditions obtain, and Sager (1963; Fig. 9) shows that tidal currents of 2 knots or greater are rather commonly encountered on the European shelf, especially in the Irish Sea and English Channel. However, bearing in mind the inherent imprecision of the seabed drifter technique the error will probably be insignificant in cases where lift-off is occurring on both flood and ebb tides, since the reciprocal errors will tend to cancel out. The error will only be serious in the special case where the flood tide (say) exceeds the lift-off threshold and the ebb tide does not. In view of this it is thought inadvisable to compensate for the "misbehaviour" of the standard drifter at high current speeds by adding extra ballast since even if it were possible to ballast the drifter to take account of strong currents in the release area, the drifter may well pass into areas of weaker peak currents during its long period of drift, where the returns would again be biased.

Equally, it may well be that the drifter is being used to determine the dispersion rate of pollutants (say) rather than the bottom drift *per se* and in these cases the "uncorrected" drifter returns will probably give a closer approximation to the behaviour of the pollutant, since the pollutant may also be expected to rise into midwater depths under conditions of strong turbulence. For example, in their study of the dispersion of sewage sludge from London, the Hydraulics Research Station, Wallingford (Anon, 1968, p. 6) note that "The sludge particles ... are borne up to the surface by the large buoyancy flux of the discharge and, even after settlement to the bed, late resuspension by wave and current action will distribute them over the entire water depth with some bia towards the bottom because of their weight. Thus their motion is determined more by the entire water body movement rather than that of the lower layers alone." Certainly, in a study of sludge dispersion from a dump site in Liverpool Bay, a good general agreement was found between the ultimate distribution of labelled sludge and the recovery pattern for seabed drifters (Anon, 1972), suggesting similar behaviour during dispersion.

In keeping with the seabed drifter's role as a valuable but imprecise indicator of residual water movements, it is clearly impracticable to suggest that the above description of drifter behaviour should be used to "correct" drifter returns for "misbehaviour" in strong tidal currents. This would, in any case require a much more rigorous characterisation o drifter performance than this restricted series of fiel observations can supply. Nevertheless it is suggeste that these observations of drifter performance ma aid the interpretation of anomalous drifter returns i areas of strong tide and coupled with this, it is als suggested that closer attention might be given to th routine ballasting of drifters in the laboratory t ensure that they show only a small variability abou the standard net weight of 1 g.

Conclusions

1. The standard seabed drifter will accurately reflec near-bottom water movements in shelf area where the tidal current at midwater depth is les than 2 knots.
2. In tidal streams stronger than 2 knots the drifte may lift from the near-bottom layer to glide a midwater depth for extended periods of time.
3. It is not considered desirable to counteract thi tendency by adding extra ballast to the drifte

since this will adversely affect the drifter's performance at low current speeds, and since the errors due to lift-off will tend to cancel out on reciprocal flood and ebb tides.

A knowledge of the drifter's tendency to lift from the sea bed may aid the interpretation of anomalous drifter returns in areas of strong tidal current.

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Experiments on the survival, growth and yield of relaid seed mussels (*Mytilus edulis* L.) in the Menai Straits, North Wales

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The survival, growth and yield of young mussels relaid on small plots, at densities of 8·75 and 13·25 kg/m^2 live weight, were studied at low-water mark of spring tides in the Menai Straits, North Wales. Populations grew from mean lengths of 27 mm to minimum market size (50 mm) in 15–20 months, and to 55–58 mm in two years, but good growth was offset by high mortality so that no significant gains in live crop weight resulted. Heavy predation by shore-crabs (*Carcinus maenas* (L.)) upon mussels smaller than 45 mm shell length was the major factor restricting crop growth. During the first year, mortality of unprotected mussels was very high (70–85%), whereas losses within crab-proof cages were significantly less (17–41%). Second-year mortality on open plots fell significantly to 22–57%, most losses then being caused by storms and bird predators, but that in cages rose to 27–54% due to overcrowding and smothering in biodeposits ('mussel-mud').

Dry-flesh biomass (ash-inclusive) of unprotected mussels amounted to 4–6% of live crop weight (shell inclusive) and fluctuated seasonally, attaining peak values in late summer and early autumn. Standing crops were usually between 0·4 kg/m^2 and 0·8 kg/m^2, with a maximum of 1·2 kg/m^2. Total production of dry-flesh over the two year growing period was 0·75–1·43 kg/m^2, most production (about 69%) occurring in spring and summer of the first year. For optimum utilisation of mussel stocks and cultivation grounds the relaid mussels should be harvested at peak biomass, in late summer and autumn, and at a smaller size (45–50 mm) than at present.

Introduction

The annual production of British mussel fisheries during 1966–73 ranged between 3300 tonnes and 5500 tonnes live-weight (average 4400 tonnes), of which approximately one third was produced by cultivation. The only cultivation method employed in Britain is seabed or bottom culture, which involves the transplanting (relaying) of small mussels from natural stocks onto 'lays' situated in sheltered estuarine waters with a firm mud substrate, favourable currents and ample food supply (Davies, 1970; Mason, 1972). Mussels are thus cultivated at seven sites in England and Wales, of which the most important is the Menai Straits where mechanised systems, involving large dredgers, are used to relay and harvest the crops. In the remaining areas cultivation is small-scale and based on traditional relaying methods (Davies, 1970).

The size at which mussels are relaid in Britain varies widely but usually they are 20–40 mm in length and known as 'seed' mussels. With no mortality, one tonne of 30 mm mussels would yield about eight tonnes at a marketable size of 60 mm. However, commercial yields usually fall far below this theoretical return. In Holland, one tonne o seed mussels yields a little over one tonne of marketable crop (Davidse, 1971). In the Danish Wadde Sea the return ratio is usually below 1:1, even whe mussels are relaid at 45–50 mm length (Theisen 1968). Similar low yields are experienced in Britai suggesting that most of the weight gain from goo growth is offset by very heavy mortality. High losse of relaid seed and a general scarcity of seed mussel are the two main biological factors depressing th productivity of mussel culture grounds in Britai

In order to gain a better understanding of th growth and mortality processes operating withi relaid mussel populations, a study was made in th Menai Straits, from 1971 to 1974, of survival an yield at different relaying densities. Particular a tention was given to identifying the major sources mortality, which previous experience indicated wou probably be predators, especially the shore-cra *Carcinus maenas*. This paper presents the results the three year study, the preliminary findings havi been reported by Edwards (1973).

There have been several previous studies of *Mytil* *edulis* in the Menai Straits. Settlement, growth ar meat condition of sublittoral populations were d ribed by Davies (1969, 1974) and by Dare and avies (in press). Growth and meat content in the arby Conwy Estuary were studied by Baird (1966) d Dare and Edwards (1975).

Materials and Methods

e site chosen for the work was the laboratory's ld station at Tal-y-foel, Anglesey, a sheltered shore ar the southern end of the Menai Straits. In Oc- ber 1971 four experimental plots (A, B, C, D) were arked out on a firm mud substrate at the mean v-water mark of spring tides, equivalent to a 5% posure level. Each plot measured 50 m^2 (10×5 m) d was subdivided into two equal subplots of 20 m^2 ×5 m) separated by a central strip of 2 m×5 m. ch central strip held two predator-proof cages, area 2 m^2, for a comparison of the mortality rates protected mussels with those exposed on the open ots. One type of cage gave protection only from rds and the other from shore-crabs as well as birds. nfortunately, the bird-proof cages – a cover of net- g suspended 15 cm above the ground and with en sides – became fouled badly by drifting weeds d had to be discontinued after three months. The ner type of cage, here called a crab-proof cage, mprised a wooden frame (2 m×1 m and 23 cm gh) with its top and sides covered with 20 mm ameter plastic mesh to exclude those *Carcinus* (of rapace width > 30 mm, see Walne and Dean, 72) capable of opening the experimental mussels.

In early November 1971 0-group mussels of 27·6 n mean length (range 15–37 mm) were obtained m near low-water of spring tides on the Roose- ck beds in Morecambe Bay, an area of potential portance for restocking mussel lays in North Wales are, 1973). The plots were stocked at two different nsities: two plots (A and C) with 200 kg of mussels d associated debris (shells, weeds) per subplot ≡ 100 tonnes/hectare) and two plots (B and D) th 300 kg per subplot (≡ 150 tonnes/ha). The ight of debris was estimated, by analysis of sam- s, as 12% of the relaid material. Thus, the true antities of live mussels put down were 175 kg on ots A and C (≡ 8·75 kg/m^2) and 265 kg on plots and D (≡ 13·25 kg/m^2). The crab-proof cages re stocked proportionately, i.e. with either 17·5 kg 26·5 kg of live mussels.

A second relaying experiment was begun in late igust 1973, this time using 0-group seed of 26·8 mm an length (range 16–39 mm) from the Heysham ds at Morecambe Bay. As in 1971, the mussels re gathered and relaid carefully by hand and rake good condition within 36–48 h. The lay-out and stocking density of plots (E, F, G, H) and cages were identical to those in the 1971 experiment, except that an additional series of four plots (W, X, Y, Z) was relaid further upshore at the 12% exposure level, i.e. slightly below low-water mark of neap tides, for comparison.

In the main experiment, November 1971–January 1974, mussels from one of each pair of 20 m^2 subplots i.e. subplots A_1, B_1 etc., and from the crab-proof cages, were sampled monthly to determine length frequency and mean individual live weight and dry flesh weight in each population. The remaining subplots (A_2, B_2 . . .) were sampled only at near-yearly intervals, to act as controls and to indicate possible mortality due to sampling disturbance. Samples from cages were returned intact, but part of each sample from the subplots was analysed for dry flesh weight. In addition, at three- or four-month intervals all the mussels on subplots A_1, B_1, C_1 and D_1, and from the cages, were lifted, washed and weighed in the field in order to measure changes in total crop weight and hence, from mean individual live weight data, the total numbers of mussels surviving in each population. The product of number of individuals and the appropriate mean individual dry flesh weight then gave an estimate of dry biomass on each subplot. Subplots A_2, B_2, C_2 and D_2 were assessed similarly in October 1972 and November 1973. Similar procedures were used on the second series of plots from August 1973 until the premature termination of this experiment in January 1974.

Shell lengths were measured with calipers to the 1 mm below, with a 0·5 mm grouping correction added to the calculated means. The field weights of crops were corrected for debris (empty shells and weeds) by laboratory analysis of subsamples. Dry flesh weight was determined at standard lengths (20, 25, 30 . . . mm each ± 1 mm). The meats were removed from shells, macerated, and then three replicated batches of ten meats were oven-dried on tared filter papers at 100°C for 24 h, after which there was no significant further reduction in weight. Shell weights were measured at the same standard lengths by oven-drying at 100°C for 4 h.

From regressions of weight on length each month the dry flesh and shell weight at the population mean length could be calculated.

The relative abundance of the shore-crab population was monitored each month using pots baited with salted fish over a standard two-day trapping period. Twelve pots were set around the perimeter of each series of four plots, and the catches over two successive 24 h periods recorded. The pots, which were selective for crabs above 30 mm carapace width, measured 30×45×25 cm and consisted of rectangu-

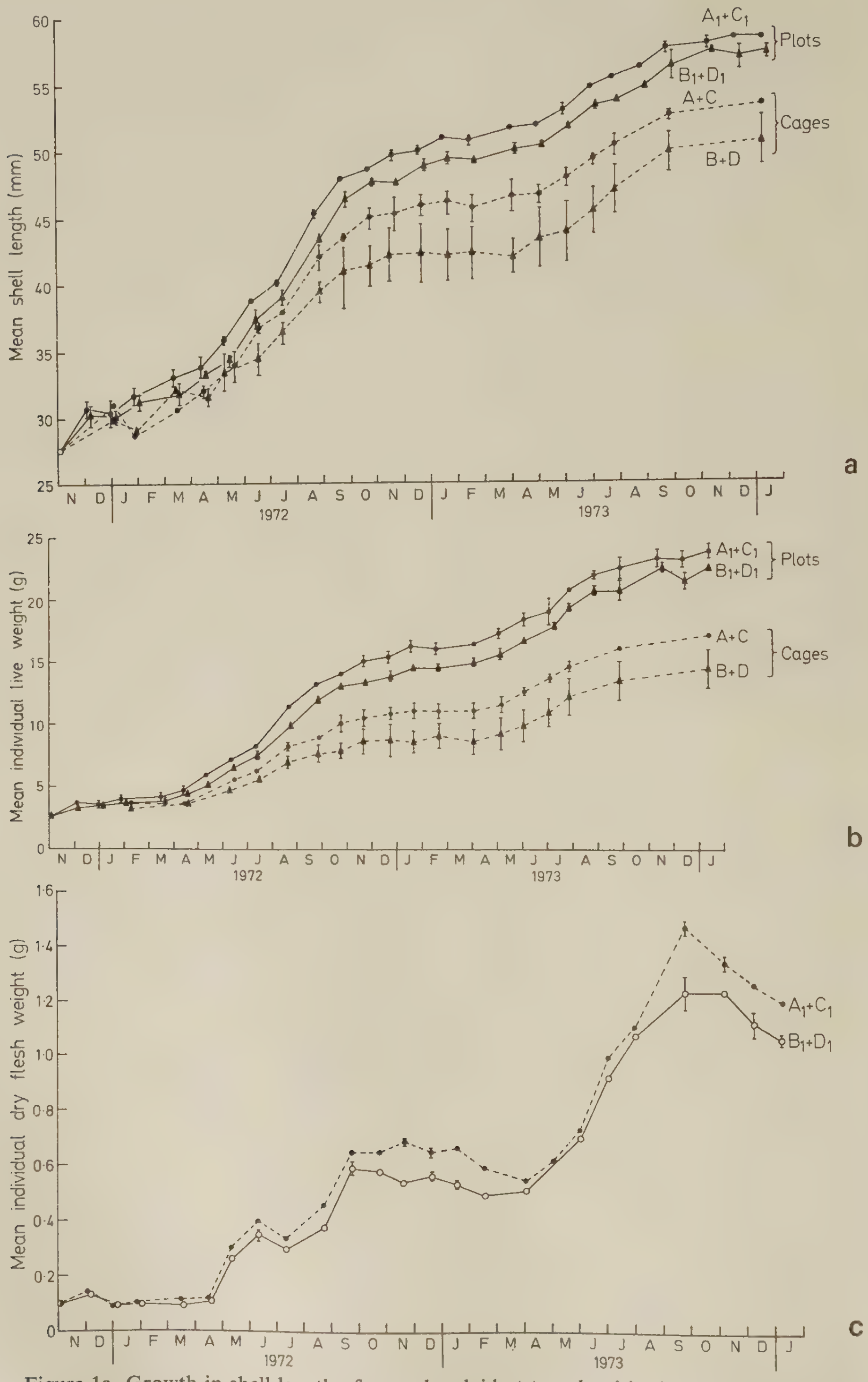

Figure 1a. Growth in shell length of mussels relaid at two densities in the Menai Straits (Tal-y-foel) at low-water mark of spring tides. A + C = lower density populations, B + D = higher density populations. Each vertical bar denotes the range of two observed results. Figure 1b. Mean individual live weights of mussels. See caption to Figure 1a. Figure 1c. Mean individual dry flesh weights of mussels. See caption to Figure 1a.

metal frames covered with 10 mm galvanised wire ting and having an 8 cm diameter funnel entrance he top.

Results

Growth

owth curves of mean shell length, individual live ight and individual dry flesh weight of mussels open plots and in cages are shown for the 1971 periment in Figure 1. Data for the 1973 repeat periment, which lasted only four months, are not own. Growth was markedly seasonal, being fastest m May to September but slowing often to scarcely ectable levels in winter, December–March, when flesh weight actually decreased (see later).

inear growth was much faster on open plots than cages (Fig. 1a) with strong indications of an erse correlation with population density. On ts B and D, the mean lengths of all populations attained the minimum legal market size (50 mm) hin approximately 20 months after relaying, those lower-density plots (A and C) having achieved length in only 15 months. By the autumn two rs after transplanting most unprotected mussels e harvestable, at 55–58 mm mean length. In con- st, mussels in three of the cages took 21–23 months each minimum size while in the fourth cage the an length was still only 48 mm after two years.

Table 1. Values of the asymptotic mean length (L_∞) and the instantaneous growth coefficient (K) for relaid mussels on open plots and in cages at mean low-water mark of spring tides, Tal-y-foel

		Open plots		Cages	
		L_∞	K	L_∞	K
Lower density...	A	62·38	0·9632	57·28	0·9194
	C	61·80	1·0206	59·97	0·7433
Higher density...	B	62·58	0·8109	65·24	0·5228
	D	62·32	0·9215	77·50	0·2578

Values of the asymptotic mean length (L_∞) on the open plots were all between 61·8 mm and 62·6 mm, with instantaneous growth coefficients (K) of 0·81 to 1·02 (Table 1), but results were much more variable in cages due to reduced growth and overcrowding. These parameters were calculated according to the method of Beverton and Holt (1957) using length data taken in January 1972, 1973 and 1974 when shell growth was minimal.

The slower growth in cages may be attributed to restricted food availability, exacerbated by some measure of overcrowding due to better survival, and this was reflected more strikingly by the mean individual live weights (Fig. 1b). At the end of the experiment, mussel populations on open plots had mean individual weights in the range 22–25 g whereas

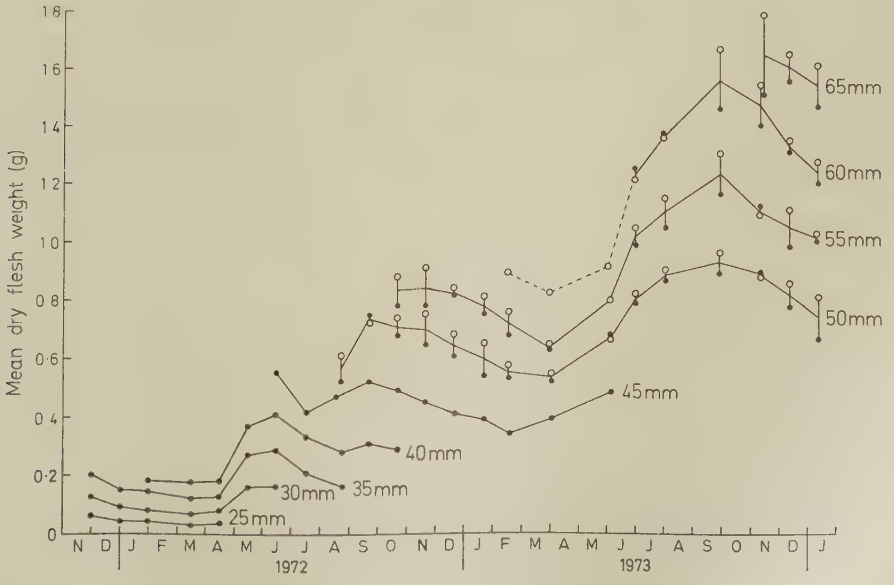

Figure 2. The annual cycle in total dry flesh weight of mussels of standard lengths on the low intertidal plots at Tal-y-foel, Menai Straits. For mussels ⩾ 50 mm, values for lower density populations (A_1 + C_1) are shown by open circles, and values for higher density populations (B_1 + D_1) are shown by filled circles.

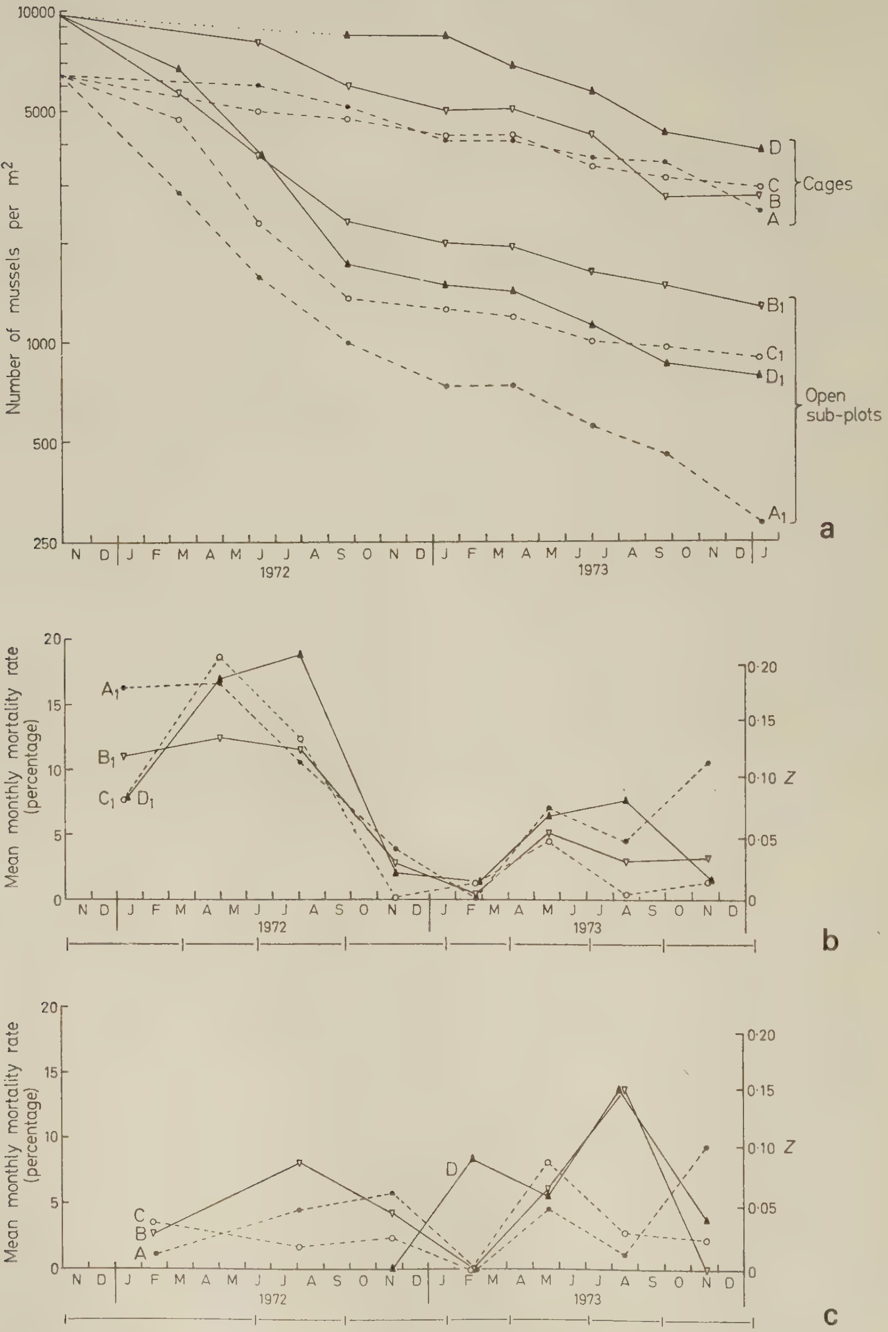

Figure 3. Survival and mortality rates of relaid mussels at Tal-y-foel, Menai Straits, on exposed plots and within crab-proof cages: (a) survival curves in numbers of mussels per m², (b) seasonal changes in the mean monthly mortality rate on exposed plots, and (c) in crab-proof cages. Broken lines refer to initial lower density populations (A and C), continuous lines to higher density populations (B and D).

ose in cages were only 12–17 g. The live weight owth curves are very similar to those for shell ngth, but their apparent smoothness and confor- ity with the latter mask the more complex, true owth pattern revealed by considering dry flesh eight (Fig. 1c).

Mean individual flesh weight fluctuated sometimes ut of phase with shell growth. It increased rapidly om April to September, except for a reversal in une–July 1972, but during winter it either remained eady (1971–72) or decreased (by 10–15% in 1972 73, and at least 10–15% in 1973–74), suggesting dverse feeding conditions. The 1972 mid-summer ll in flesh content coincided with a sharp decline the diatom, flagellate and chlorophyll α concentra- ons in the local inshore waters (M. Helm and F. mith, personal communication). The seasonal varia- on in dry flesh content of mussels of standard ngths on open plots (Fig. 2) shows, for animals 45 mm length, maximum values in early autumn eptember–October) followed by a steady decline rough the winter to minimum levels in early spring. he average winter loss in weight was 28·5% in 1972– 3 and 19·1% for that part of the 1973–74 winter p to January. In 1971–72 the 25–35 mm group had so lost weight (by about 46%). Figure 2 also indi- ates that for a given length, in the 50–65 mm range, e flesh content was generally higher in the lower nsity populations, particularly in winter. Among naller mussels the same tendency occurred, but the fferences were too small to illustrate in Figure 2. Thus, with respect to all three parameters of growth, the mussels performed better at the lower density, while growth of mussels protected in cages was markedly worse than that of unprotected animals.

Survival

First experiment, 1971–74: Survival curves for the various plot and cage populations set out in November 1971 are shown in Figure 3a; mortality rates are summarised in Table 2, as instantaneous coefficients of total mortality (Z), and are illustrated seasonally in Figures 3b and 3c. Unprotected mussels suffered very high losses, averaging 78·7% (range 70–85%) for all eight subplots in the first year, 37·7% (range 22–57%) in the second year, and 86·7% (range 79–93%) over the two-year cultivation period. The fall in mortality rate in the second year was highly significant ($P < 0{\cdot}01$, 't' test and F ratio) but there was no significant difference in either year between high- and low-density plots nor between subplots measured annually (A_2, B_2 ...) and those lifted for weighing and sampling at frequent intervals (A_1, B_1 ...). However, Table 2 indicates consistently lower annual mortality rates on the less disturbed series of subplots. Although this trend is significant by the sign-test ($P < 0{\cdot}01$, $n = 8$, $r = 0$) most of these differences can be accounted for by the removal of samples for dry weight analysis. The average difference, expressed as instantaneous coefficients of total mortality, between the two series was 0·206 in year I and 0·220 in year II, of which 'sampling' mortality amounted to values of Z of 0·136 and 0·174 respectively.

ble 2. Annual mortality of 1971-relaid mussels on open plots and in crab-proof cages, expressed as instantaneous coefficients of total mortality (Z) and as equivalent percentages. * plots and cages stocked initially at the higher density (13·25 kg/m²), others at 8·75 kg/m²

Mussel population		Year I		Year II		Total mortality for two years	
		Z	%	Z	%	Z	%
pen plots:							
Subplots	A_1	1·877	84·7	0·836	56·7	2·713	93·4
	$*B_1$	1·440	76·3	0·455	36·6	1·895	85·0
	C_1	1·541	78·6	0·353	29·7	1·894	85·0
	$*D_1$	1·742	82·5	0·684	49·5	2·426	91·2
	av.	*1·650*	*80·8*	*0·582*	*44·1*	*2·232*	*89·3*
	A_2	1·529	78·3	0·346	29·2	1·875	84·7
	$*B_2$	1·210	70·2	0·344	29·1	1·554	78·9
	C_2	1·415	75·7	0·251	22·2	1·666	81·1
	$*D_2$	1·621	80·2	0·509	39·9	2·130	88·1
	av.	*1·444*	*76·4*	*0·363*	*30·4*	*1·806*	*83·6*
	av.	*1·547*	*78·7*	*0·473*	*37·7*	*2·019*	*86·7*
ages	A	0·445	35·9	0·313	26·9	0·758	53·1
	*B	0·527	41·0	0·770	53·7	1·297	72·7
	C	0·362	30·4	0·423	34·5	0·785	54·4
	*D	0·183	16·7	*0·702*	*50·4*	*0·885*	*58·7*
	av.	*0·379*	*31·5*	*0·552*	*42·4*	*0·931*	*60·6*

Mortality was very significantly lower in cages, than on open plots ($P < 0{\cdot}01$) in the first year, average 31·6% (range 17–41%), but not in the second year when mortality averaged 42·6%. The two-year mortality in cages, at 60·6% average, was significantly less than on open plots ($P < 0{\cdot}01$, '*t*' test and *F* ratio). The first- and second-year losses in cages did not differ significantly from each other, and a difference between high- and low-density cages occurred only in the second year ($P < 0{\cdot}05$, '*t*' test and *F* ratio).

Figure 3b shows changes in the mean monthly death rate of unprotected mussels during successive periods, derived from the data for Figure 3a. Trends were similar on all subplots, with a high first-winter mortality rate increasing further to a peak in spring or summer before falling quickly during late summer and autumn. Second-winter losses were very low, but there followed another increase in mortality during the second spring and summer. In cages (Fig. 3c) no such clear seasonal pattern is evident, although the significantly lower first-year, but similar second-year, mortality compared with open plots is apparent.

Second experiment, 1973: Mortality was so high on the plots relaid in late August 1973 that this experiment was curtailed after only four months. Table 3 summarises the losses on plots and in cages during the first 3½ months to mid-December 1973.

Mortalities on the plots (F, G, H, I) at the lower shore level (5% exposure) averaged 96·5% compared with 72·7% (range 65–86%) on the higher level (12% exposure) plots (W, X, Y, Z), the difference being highly significant ($P < 0{\cdot}01$, *F* ratio). As in the first experiment, there was no difference between plots stocked at high and low densities. Mussels in cages survived significantly better (*F* ratio, $P < 0{\cdot}01$) at both shore levels, although losses still averaged 27% (16–35%) at the upper level. Crabs entered two cages (G and I) at the lower level when these were damaged by a storm soon after the experiment began. The crabs remained undetected, buried in mud, until the

Table 3. Mortality of 1973-relaid mussels in the first 3½ months on open plots and in crab-proof cages at two shore levels, 5% and 12% exposure, September–December 1973; expressed as instantaneous coefficients of total mortality (*Z*) and as equivalent percentages. * plots and corresponding cages stocked initially at the higher density (30 kg/m²), others at 20 kg/m². ⁺ cages G and I were damaged by storm and thus crabs were able to enter (see text above)

Mussel population		Open plots *Z*	Open plots %		Cages *Z*	Cages %	
Lower shore level:							
Subplots	F_1	5·3	99·5				
				F	0·181	16·6	
	F_2	2·841	94·2				
	*G_1	3·1	95·5				
				G	2·993	94·7⁺	
	*G_2	2·981	94·9				
	H_1	2·900	94·5				
				H	0·248	22·0	
	H_2	2·258	89·5				
	*I_1	2·985	94·9				
				I	0·739	52·2⁺	
	*I_2	4·5	98·9				
	av.	*3·358*	*96·5*		*0·215*	*19·3*	F and H only
Higher shore level:							
	W_1	1·961	85·9				
				W	0·215	19·3	
	W_2	1·402	75·4				
	*X_1	1·060	65·4				
				X	0·176	16·1	
	*X_2	1·194	69·7				
	Y_1	1·107	66·9				
				Y	0·412	33·8	
	Y_2	1·229	70·7				
	*Z_1	1·093	66·5				
				Z	0·436	35·3	
	*Z_2	1·346	74·0				
	av.	*1·299*	*72·7*		*0·310*	*26·7*	

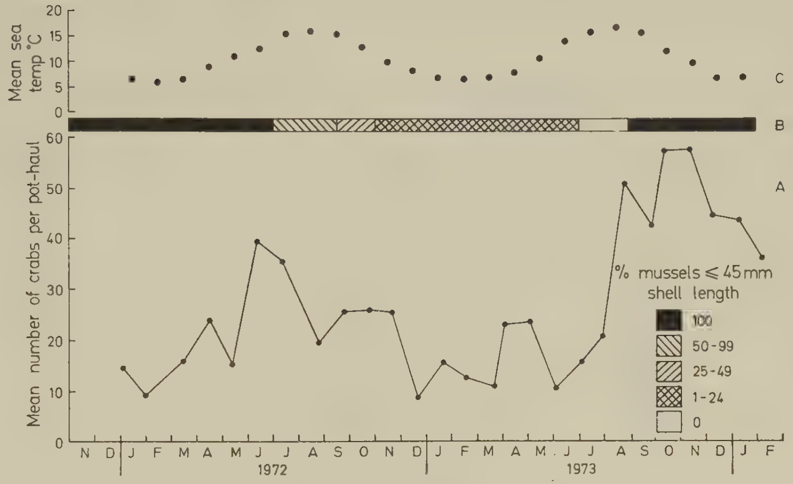

Figure 4. Seasonal abundance of shore-crabs (A) at Tal-y-foel, Menai Straits, in relation to (B) the availability of vulnerable (≤45 mm) mussels, and (C) the sea temperature at Menai Bridge.

id-December inspection when 75 medium and large rabs (46–80 mm carapace width) were found, 63 in age G and 12 in cage I. The very high mortalities in ese two cages are thus further evidence of the vulerability of seed mussels to *Carcinus* predation. In e two undamaged cages (F and H) the losses were milar to those in the upper level cages.

Causes of Mortality

) *Physical factors*. Mortalities arising directly from e relaying operations could not be measured but ey appeared to be slight, judging by the appearance plots and caged mussels a few days after the start each experiment. Small losses from tidal scouring plots in rough weather were evident occasionally. the first winter, scouring was limited mainly to a orner of subplot A_1, while both halves of A and D ere thinned lightly during the second summer and utumn. Deaths from smothering in mud were considered to be unimportant on plots, which were very able and accreted "mussel-mud" only slowly, but me mortality undoubtedly resulted from the periodlifting, weighing, and respreading of subplots A_1, , C_1 and D_1. In cages, on the other hand, smotherg was probably the primary cause of mortality, pecially in the second year when populations were ticeably overcrowded and deposition of mud was tremely heavy; as much as 0·3 m of "mussel-mud" d to be removed from cages at every three- or ur-monthly weighing operation.

) *Predators*. In the absence of obvious major ysical mortality factors, the contrasted survival patterns of exposed and protected mussels strongly suggest that predators were the most important cause of loss on plots in the first year. Bird predation was greatly restricted by the low exposure level and by our own activities, field-work occupying half the spring-tide ebb periods. Oystercatchers (*Haematopus ostralegus* L.) regularly fed on the mussel plots in autumn and winter though not more than four birds were seen opening mussels during any low-tide period. One or two Herring Gulls (*Larus argentatus* Pontopp.) occasionally took small mussels. Bird predation, therefore, was considered slight in the first year but probably more important in the second year when mussel numbers were much lower.

There was abundant evidence to incriminate *Carcinus* not only as the major predator throughout the first year after relaying but also as the main cause of the high mortality of young mussels. Numerous crushed and chipped mussel shells, showing typical crab damage, were seen on and around the 1971-relaid plots during the first year. However, much more striking evidence was afforded by the second experiment. Within days the mud was littered with broken shells and these increased in quantity as the plots were rapidly thinned. A similar picture occurred in the two cages (G and I) which crabs were able to enter.

Shore-crabs were numerous at Tal-y-foel in every month of the study though varying widely in seasonal abundance (Fig. 4). From January 1972 to April 1973 numbers caught per pot-haul were correlated positively with local sea-temperature at Menai Bridge, 12 km from Tal-y-foel ($r = 0{\cdot}6275$, 14 df,

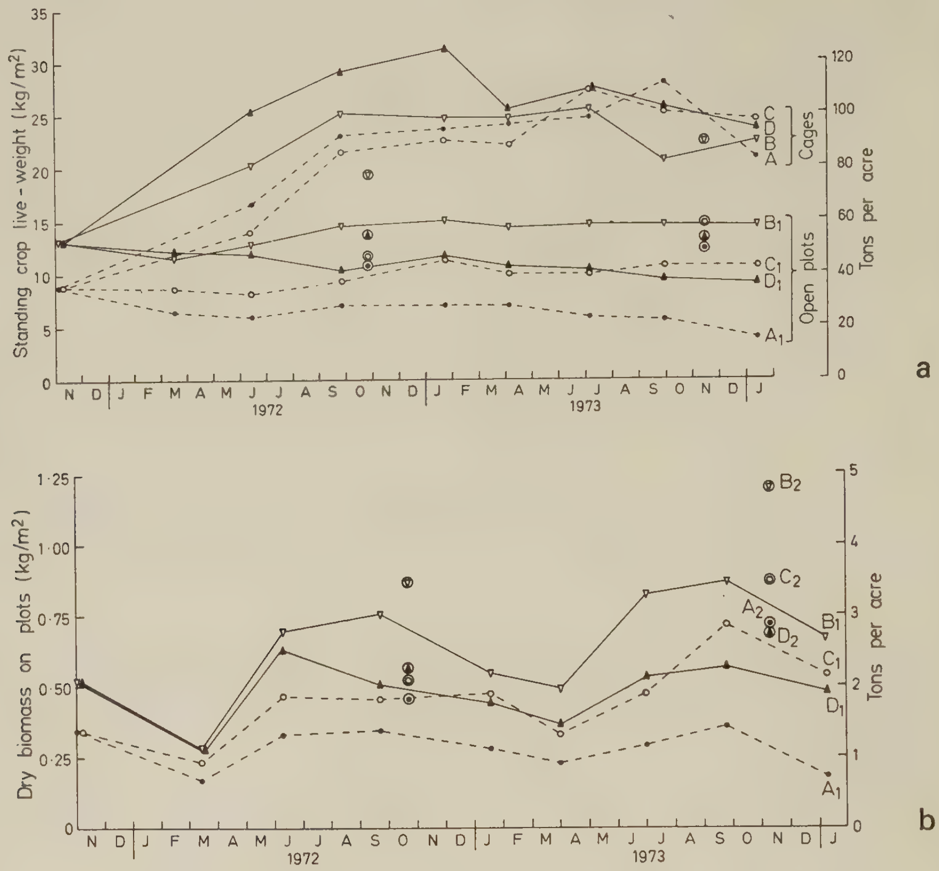

Figure 5. Changes in the standing crops of relaid mussels at Tal-y-foel, Menai Straits: (a) gross live-weight per m² on plots and in cages, (b) dry flesh biomass on unprotected plots. Lower initial density populations (A and C) are denoted by broken lines, and higher density populations (B and D) by continuous lines. Encircled values for October 1972 and November 1973 refer to the annually sampled subplots A_2, B_2, C_2 and D_2.

$P < 0{\cdot}01$), but no overall correlation obtained between May 1973 and January 1974. The high mortality of 1973-relaid mussels coincided with a large and rather late influx of crabs to the plots in late summer and autumn. The influx started in August just before the plots were stocked (Fig. 4).

Field experiments at Tal-y-foel in summer 1972, in which crabs of 60–75 mm carapace width were placed in cages with samples of mussels from the plots, showed that large *Carcinus* could open successfully plot mussels of up to 45 mm length. These results agreed closely with the earlier observations of G. Davies (unpublished data) who exposed Menai Straits mussels, taken from a low intertidal level, to crabs in a large outdoor tank at Conwy. Taking 45 mm as the upper limit for crab predation at Tal-y-foel, the percentage of mussels below 46 mm on the plots, and hence at risk, each month is shown in Figure 4. All the 1971-relaid mussels were theoretically vulnerable to crabs for the first eight or nine months until, between July and October, the high summer growth rates enabled the majority of survivors to grow rapidly beyond the high-risk phase. Although mussels of less than 46 mm were present on plots for a further nine months, they were relatively scarce and many might have been protected within the tightly embyssed mussel clumps.

Standing crops

The standing crop is expressed both as live (gross) weight of mussels and as dry biomass of flesh per uni area. The latter is the product of the mean individua dry flesh weight and the population density.

ble 4. Standing crops of 1971-relaid mussels, expressed as kg/m² live-weight, on open plots and in crab-proof cages at the start of the experiment (W_0), after 1 year (W_1) and 2 years (W_2) with annual and total increments in yield.

ote: Subplots A_1 .... D_1 and the cages were disturbed regularly for sampling purposes; subplots A_2 .... D_2 were disturbed only at yearly intervals

		Live-weight (kg/m²)			Yield increment ratios		
					Annual		Final
		W_0	W_1	W_2	W_1/W_0	W_2/W_1	W_2/W_0
pen plots							
Subplots	A_1	8·75	7·0	5·0	0·80	0·71	0·57
	B_1	13·25	14·3	14·5	1·08	1·01	1·09
	C_1	8·75	10·0	10·5	1·14	1·05	1·20
	D_1	13·25	10·75	9·25	0·81	0·86	0·70
	av.				*0·96*	*0·91*	*0·89*
	A_2	8·75	10·75	12·25	1·23	1·14	1·40
	B_2	13·25	19·25	22·5	1·45	1·17	1·70
	C_2	8·75	11·5	14·5	1·31	1·26	1·66
	D_2	13·25	13·5	13·75	1·02	1·02	1·04
	av.				*1·25*	*1·15*	*1·45*
	av.				*1·11*	*1·03*	*1·16*
ges	A	8·75	23·0	25·25	2·63	1·10	2·89
	B	13·25	25·0	21·0	1·89	0·84	1·58
	C	8·75	21·75	24·75	2·49	1·14	2·83
	D	13·25	29·5	24·75	2·23	0·84	1·87
	av.				*2·31*	*0·98*	*2·29*

Live-weight. Crops of 1971-relaid mussels on un-
otected plots did not change significantly in live-
ight during the two-year growth period to harvest-
le size in autumn 1973 (Fig. 5a). Growth more
less compensated for the high mortality, and
anges after two years were within the range +70%
–43%, averaging +16% (Table 4). Crops on the
atively undisturbed subplots (A_2, B_2, ...) were
nsistently, though not significantly, heavier than
the frequently disturbed subplots (A_1, B_1, ...).
gure 5a also shows strikingly the benefits of pro-
ction from crabs. Protected crops each year were
gnificantly heavier than unprotected crops on cor-
sponding plots. By the end of the vulnerable first
ar, caged crops showed significant weight gains of
% to 163% (average 131%). In the initially more
htly stocked cages (A and C) the crops had nearly
bled by harvest time, at the end of the second year,
t in the more heavily stocked cages (B and D)
ere was a fall in crop weight in the second year due
vercrowding. Overall, there was no significant
ange in weight during the second year in cages.
nal protected yields were equivalent to densities of
0–275 tonnes/ha (80–110 tons/acre), close to the
aximum we have observed in natural mussel popula-
ons, in Morecambe Bay (low intertidal zone) and
e Menai Straits (sublittoral population of one
ar-class).

) *Dry biomass.* The dry-flesh biomass of the un-
otected 1971 crops showed marked seasonal fluctuations (Fig. 5b). Maximum biomass occurred in late summer and early autumn, and was followed by a decline from late autumn to early spring with subsequent recovery due to rapid summer growth. Consequently, when comparing changes in biomass during the individual years of such an experiment, the results can be affected by annual variations in the timing and magnitude of the flesh-condition cycle. In the present study, the values to be compared (Table 5) are those for early November of each year (i.e. W_0, W_1, and W_2) and are thus close to the annual maxima.

Biomass yields showed a pattern similar to those of live-weight except that over the two years there was a significant increase (doubling) in biomass on the less disturbed subplots (A_2, B_2 ...) which was not revealed by live-weight data. The annual gains of biomass, however, were not themselves significant. The small average gain (34%) on frequently disturbed subplots (A_1, B_1 ...) was not significant. Biomass was not significantly affected by initial relaying densities (probably insufficient contrast) or by the experimental disturbance, although the less disturbed subplots held a consistently higher biomass. The biomass of protected mussel populations was not measured because of insufficient material, but the trends in cages probably paralleled the significant doubling of the live-weight noted above.

Figure 5 shows that a dry biomass of 0·4–0·8 kg/m² was sustained on most subplots for much of the time,

Table 5. Dry biomass of 1971-relaid mussels on open plots at the start of the experiment (W_0), after 1 year (W_1) and 2 years (W_2), with annual and final increments in yield.
Note: Subplots A_1 .... D_1 were disturbed regularly for sampling purposes; subplots A_2 .... D_2 were disturbed only at yearly intervals

		Dry biomass (kg/m²)			Yield increment ratios		
					Annual		Final
		W_0	W_1	W_2	W_1/W_0	W_2/W_1	W_2/W
Subplots	A_1	0·34	0·33	0·30	0·97	0·91	0·88
	B_1	0·52	0·69	0·80	1·33	1·16	1·54
	C_1	0·34	0·46	0·65	1·35	1·41	1·91
	D_1	0·52	0·49	0·54	0·94	1·10	1·04
	av.				*1·15*	*1·15*	*1·34*
	A_2	0·34	0·46	0·72	1·35	1·57	2·12
	B_2	0·52	0·86	1·19	1·65	1·38	2·29
	C_2	0·34	0·52	0·87	1·53	1·67	2·56
	D_2	0·52	0·56	0·68	1·08	1·21	1·31
	av.				*1·40*	*1·46*	*2·07*
	av.				*1·28*	*1·30*	*1·71*

with a maximum of 1·2 kg/m². Dry biomass comprised on average 5·7% of the final live-weight (W_2) on plots, compared with 4·5% after one year (W_1) and 3·9% at the start of the experiment. Assuming similar proportions in protected mussels, then the corresponding final biomass levels in cages would have been 1·2–1·4 kg/m² compared with 1·0–1·3 kg/m² at the end of the first year. Actual values were probably lower, however, due to the effect of the dense crowding in cages during the second year.

For conversion to ash-free approximate values these biomass figures should be multiplied by a facto of 0·89 (Dare, in press).

Production

Terminology and the methods of computing production follow those of D. J. Crisp (in Holme and McIntyre, 1971). The results are summarised in Table 6.

Total production by the 1971-relaid mussels during their two years on unprotected and regularly disturbed subplots (A_1, B_1 ...) ranged from 0·75 kg/m² t

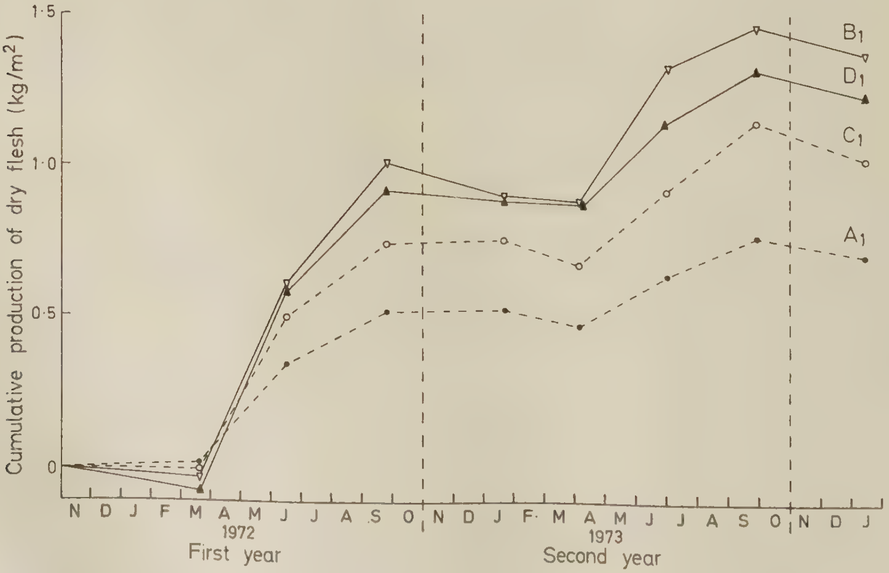

Figure 6. The production of dry flesh (in kg/m²) by relaid mussels near low-water mark of spring tide at Tal-y-foel, Menai Straits. Broken lines refer to the lower initial density subplots (A_1 and C_1), continuous lines to the higher density subplots (B_1 and D_1).

ble 6. Production of dry flesh, in kg/m^2, by 1971-relaid mussels on open plots, together with corresponding *P/B* coefficients

e: Mean biomass values for the *P/B* coefficients were obtained from monthly estimates, using the curves of Figure 5b: –

	Year I	Year II	Overall
A_1	0·292	0·292	0·292
B_1	0·552	0·684	0·618
C_1	0·374	0·490	0·432
D_1	0·470	0·478	0·474

Production (% total) Year I	Year II	Total	*P/B* coefficients Year I	Year II	Total
0·52 (69·3)	0·23 (30·7)	0·75	1·79	0·79	2·59
0·97 (67·8)	0·46 (32·2)	1·43	1·76	0·67	2·31
0·75 (67·6)	0·36 (32·4)	1·11	2·01	0·73	2·57
0·90 (69·8)	0·39 (30·2)	1·29	1·91	0·82	2·72
(68·6)	*(31·4)*		*1·87*	*0·75*	*2·55*

3 kg/m^2, with highest production on the more vily stocked B_1 and D_1 (Table 6). Most produc- n (69%) occurred in the first year, while Figure 6 ws that production was confined virtually to the iod April–September each year, with negligible duction between October and March. The ratio production to mean biomass, the so-called *P/B* fficient (Winberg, 1971), averaged 2·55 over the o years, with annual values of 1·87 for the first r and 0·75 for the second year (Table 6). There s good agreement between the four subplots. duction was greater on the less disturbed subplots , B_2 ...), as indicated by their higher biomass els at the annual surveys (Fig. 5b), but its com- ation is prevented by the infrequent sampling edule.

Discussion

understanding of the growth and mortality pro- sses at work within relaid mussel populations is ential if yields are to be improved significantly. the present study, the growth, stock density and al yield ratios on the experimental plots were simi- to those reported from commercial fisheries.

A high (> 50%) annual mortality rate appears be characteristic of many natural and cultivated pulations of young mussels (i.e. less than two rs old) and is caused mainly by various physical tors and predators (Theisen, 1968; Seed, 1969; re, in press). At Tal-y-foel, predation by *Carcinus* s the major cause of mortality during the first year er relaying, and it is probably the most important tor depressing crop growth and final yield on low ertidal lays of young mussels in the Menai Straits. ab predation was intense on our small plots, even the high relaying density of 150 tonnes/ha, although on larger lays the predation pressure might be less. On sublittoral lays in the Menai Straits, however, sporadic invasions of starfish (*Asterias rubens* L.) can inflict heavy mortality, irrespective of size of mussels or lays, and this loss is superimposed on the toll of small mussels taken by crabs. Starfish attacks can be controlled by proper husbandry, however, whereas at present there is no practical way of significantly reducing crab predation on large cultivated areas.

The predation levels observed at Tal-y-foel, and elsewhere in the Menai Straits, necessitate a high relaying density, which is more than double that employed in Holland. However, even on the small plots there were signs of reduced shell growth rate and meat yield at higher population densities. Such adverse effects of crowding might become more pronounced on commercial lays, which can exceed 20 ha in the Menai Straits.

Standing crops and production of dry flesh at Tal-y-foel were comparable with those of some natural populations at similar shore levels in Morecambe Bay (Dare, in press) and is further evidence of the intrinsic productivity of mussel beds. For optimum utilisation, the relaid crops should be harvested in late summer and autumn when meat content is greatest. Extending the harvesting period through winter, as is normal practice in Britain, will result in reduced meat yields. The biomass data also indicate that, since there was little net increase in standing crops during the second year, consideration could be given to harvesting after only one year on lays, thereby increasing the annual output. Harvesting of smaller (45–50 mm) mussels, however, would require the development of new products and markets in Britain, although such sizes are traditionally marketed in France.

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Étude du régime alimentaire de l'Aigle de mer, *Myliobatis aquila* (L., 1758) des côtes tunisiennes

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Myliobatis aquila, the Eagle Ray, is a voracious species which feeds all the year round. The stomach contents of 523 fishes (males 281, females 241) have been examined. Benthic invertebrates are found in the stomachs more frequently than any other group: there is no specific choice for them. The proportion of teleosts in the stomach contents of *M. aquila* increases with the length of the ray. This is most evident in females which normally reach a larger size than males. The eagle ray provides an example where a change from a demersal to a semi-pelagic mode of life is associated with a change in diet which reflects the fauna of the new environment.

Introduction

régime alimentaire de l'Aigle de mer, *Myliobatis*
la (L., 1758), semble n'avoir fait, à notre con-
sance l'objet d'aucune étude approfondie.
a littérature ichthyologique mentionne som-
rement que cette espèce fouille les substrats va-
ou sablo-vaseux à l'aide de son museau pour y
cher des Invertébrés benthiques. Les groupes
ogiques les plus fréquemment consommés se-
nt les Mollusques gastéropodes et pélécypodes
es Crustacés.
ans un travail de synthèse concernant les rela-
s alimentaires entre les Sélaciens et le zoobenthos
côtes Nord de la Tunisie (Azouz et Capapé,
1), nous avons remarqué que ces groupes étaient,
ait, le plus fréquemment absorbés par *M. aquila*.
nfin lors d'une étude concernant certains aspects
a biologie de cet Hypotrême (Capapé et Quig-
i, 1974) nous avons écrit que «l'animal peut se
rrir également de Téléostéens, de Sipunculiens,
nélides polychètes et même d'Ascidies».
nous a paru intéressant d'analyser le régime
entaire de *M. aquila* en fonction des saisons, du
et de l'âge afin de contribuer à une meilleure
naissance de la biologie de cette espèce.

Matériel et méthodes

matériel examiné provient de captures faites au
lut ou au trémail le long des côtes tunisiennes plus précisément sur le littoral nord, dans les golfes de Tunis et de Gabès.

L'analyse des contenus stomacaux a toujours été faite sur du matériel fraîchement pêché et en excellent état de conservation. Nous avons observé en tout 523 individus: 282 mâles (163 jeunes, 119 adultes) et 241 femelles (125 jeunes, 116 adultes).

Pour l'étude des contenus stomacaux nous donnons:

1. le coefficient de réplétion (CR) défini comme le pourcentage d'estomacs pleins ou contenant des restes de nourriture par rapport au nombre total d'estomacs examinés.
2. l'indice de fréquence (IF) des proies qui est le rapport du nombre d'estomacs contenant un certain groupe zoologique de proies au nombre total d'estomacs pleins.

Coefficient de réplétion et indice de fréquence sont précisés pour les quatre saisons: printemps (P), été (E) automne (A), hiver (H).

Mâles et femelles sont étudiés séparément et pour chaque sexe jeunes et adultes. Sont considérés comme adultes tous les individus ayant atteint ou dépassé la taille de première maturité sexuelle.

Le long des côtes tunisiennes les mâles sont adultes à partir de 40 cm d'envergure discale, bien avant les femelles qui ne le sont qu'après 50 cm. L'installation de la puberté plus précoce chez les mâles que chez les femelles entraîne un dimorphisme sexuel de taille très important. En effet le plus grand mâle que nous

Tableau 1. Variation du coefficient de réplétion en fonction du sexe de l'âge et des saisons

Sexe	Mâles								Femelles								
Âge	Jeunes				Adultes				Jeunes				Adultes				
Saisons	P	É	A	H	P	É	A	H	P	É	A	H	P	É	A	H	Tot géné
Nombre individus....	39	42	38	44	36	24	29	30	29	44	33	19	30	36	23	27	52
Estomacs pleins.......	30	31	31	36	30	20	23	22	23	35	26	15	24	29	20	23	41
Coefficient de réplétion..	77	74	82	82	83	83	79	73	79	80	79	79	81	87	85	82	81

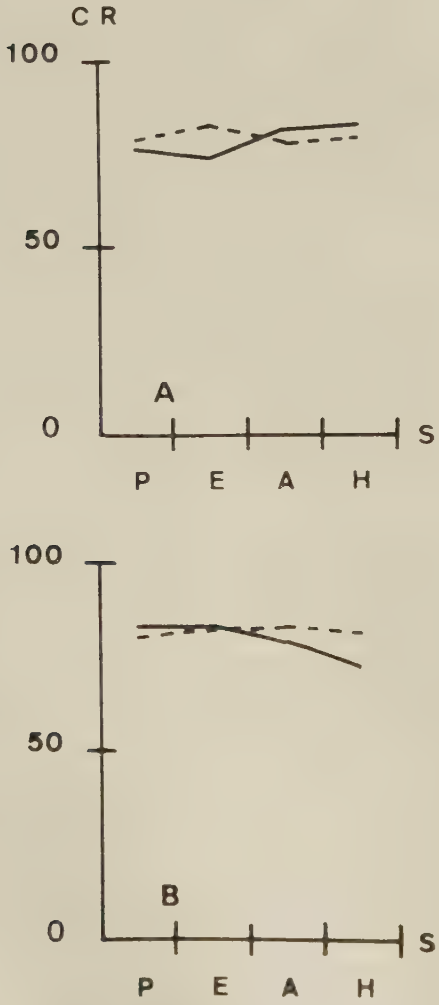

Figure 1. Mise en évidence du coefficient de réplétion (CR) durant les différentes saisons (S) printemps (P), été (É), automne (A), hiver (H).

A: individus juvéniles ------ femelles
B: adultes ——— mâles

ayons observé en Tunisie mesurait 55 cm de larg tandis que la plus grande femelle dépassait 83 (Capapé et Quignard, 1974).

Présentation des résultats

1) *Coefficient de réplétion:* Tableau 1, Figure 1
Le coefficient de réplétion est élevé pour tous individus au cours de l'année et subit peu de fluct tions saisonnières.

Les jeunes mâles s'alimentent moins que les jeu femelles en été mais plus que celles-ci en hiver. mâles adultes, par contre, consomment moins proies en hiver.

2) *Analyse qualitative et quantitative des groupes z logiques ingérés:* Tableau 2, Figure 2
Les jeunes individus mâles et femelles se nourriss essentiellement de Lamellibranches et à un de moindre d'Invertébrés benthiques comme les Ga ropodes, les Crustacés et les Annélides polychè Il est à noter, toutefois, dans les contenus gastri des femelles juvéniles, la présence de Téléostéens entrent pour une part non négligeable dans l'alim tation de ces dernières.

Les adultes des deux sexes diversifient leurs pr mais les organismes zoobenthiques précédem cités constituent la base même de leur nourrit Nous avons trouvé, par contre, plus fréquemm des Téléostéens dans les estomacs des grands ind dus. En automne et en hiver, ce groupe zoolog est même le plus représenté dans le régime alin taire des femelles.

Au niveau des groupes zoologiques en généra n'apparaît pas d'importantes variations saisonni L'indice de fréquence des Gastéropodes est élevé chez les mâles adultes en été et en auto tandis que les femelles juvéniles consomment da tage de Crustacés pendant l'automne et l'hiver. c'est principalement au printemps que l'on renco eau 2. Analyse qualitative et quantitative des groupes zoologiques ingérés en fonction du sexe, de l'âge et des saisons. Mise en évidence des indices de fréquence (IF)

A. Cas des mâles

Saisons pes zoologiques	Jeunes P	 É	 A	 H	Adultes P	 É	 A	 H
ellibranches........	30 (1)	31 (1)	31 (1)	36 (1)	20 (0·66)	12 (0·5)	11 (0·47)	14 (0·57)
éropodes..........	9 (0·30)	9 (0·29)	10 (0·29)	12 (0·33)	6 (0·20)	7 (0·35)	9 (0·39)	4 (0·16)
acés..............	8 (0·26)	9 (0·29)	8 (0·25)	10 (0·27)	6 (0·20)	3 (0·15)	6 (0·26)	4 (0·16)
ostéens............	0	0	0	0	7 (0·23)	4 (0·2)	8 (0·33)	8 (0·33)
élides.............	1 (0·03)	3 (0·09)	4 (0·14)	2 (0·05)	1 (0·03)	2 (0·1)	3 (0·13)	3 (0·12)
es groupes.........	0	0	0	0	0	1 (0·05)	1 (0·04)	1 (0·04)

B. Cas des femelles

Saisons pes zoologiques	Jeunes P	 É	 A	 H	Adultes P	 É	 A	 H
llibranches........	20 (0·83)	30 (0·89)	21 (0·81)	15 (1·00)	12 (0·50)	16 (0·55)	10 (0·52)	13 (0·56)
ropodes..........	8 (0·37)	7 (0·19)	7 (0·30)	6 (0·40)	6 (0·25)	7 (0·27)	8 (0·42)	8 (0·33)
acés..............	3 (0·12)	7 (0·19)	9 (0·35)	6 (0·40)	4 (0·16)	6 (0·24)	7 (0·37)	8 (0·33)
stéens............	3 (0·12)	4 (0·13)	2 (0·08)	2 (0·16)	10 (0·42)	16 (0·55)	12 (0·63)	13 (0·56)
ides.............	2 (0·08)	2 (0·07)	4 (0·16)	3 (0·20)	5 (0·21)	4 (0·13)	3 (0·17)	4 (0·16)
groupes.........	0	2 (0·7)	2 (0·08)	6 (0·20)	3 (0·12)	3 (0·12)	3 (0·17)	4 (0·16)

C. Ensemble des individus

Groupes zoologiques	Nombre total	IF
ibranches........	322	0·61
opodes..........	123	0·24
cés..............	104	0·20
téens............	89	0·17
ides.............	46	0·09
groupes.........	26	0·05

lative abondance des Annélides polychètes dans pareil digestif des femelles adultes.

ur l'ensemble de tous les individus (Tabl. 2C) Lamellibranches (IF = 0·61), les Gastéropodes = 0·24), les Crustacés (IF = 0·20) sont le fondet du régime alimentaire de *Myliobatis aquila* des s tunisiennes.

s Téléostéens (IF = 0·17) ne prennent une réelle portance que dans l'alimentation des «grands icus», tandis que les Annélides polychètes (IF = bien que consommés par toutes les catégories mplaires ne constituent qu'une faible partie de trition de cet Hypotrême.

nalyse spécifique des proies ingérées (Tabl. 3)

portance spécifique des proies ingérées concerne ntiellement les groupes zoologiques préférentiels: ellibranches, Gastéropodes et Téléostéens.

Dans la majorité des cas il nous a été difficile d'identifier de façon précise les individus appartenant aux Lamellibranches et aux Gastéropodes car *Myliobatis aquila* broie les coquilles pour en extraire l'animal et en rejette les débris.

Chez les Lamellibranches parmi les espèces déterminées, les plus abondantes appartiennent au genre *Chlamys* (104): ce sont surtout *Chlamys opercularis* (25), *C. varius* (22) et *C. glabra* (19).

Tapes decussatus (37), *Cardium aculeatum* (25) et *Pecten jacobaeus* (25) sont consommés également de façon fréquente.

Parmi les Gastéropodes ce sont surtout les espèces du genre *Murex* (45) que nous avons reconnues le plus souvent dans les contenus gastriques de *M. aquila*. Les Nudibranches, en général, constituent une part importante des Gastéropodes ingérés par ce Sélacien.

Les Téléostéens mangés par *M. aquila* sont soit des espèces pélagiques comme certains Clupeidae soit des espèces benthiques; parmi ces dernières il faut retenir différents *Gobiidae* et certains Pleuronectiformes.

M. aquila capture de nombreuses autres espèces faisant partie de divers groupes zoologiques mais ces prises semblent être occasionnelles ou accidentelles et ne constituent pas la base de son alimentation.

FIG. 2

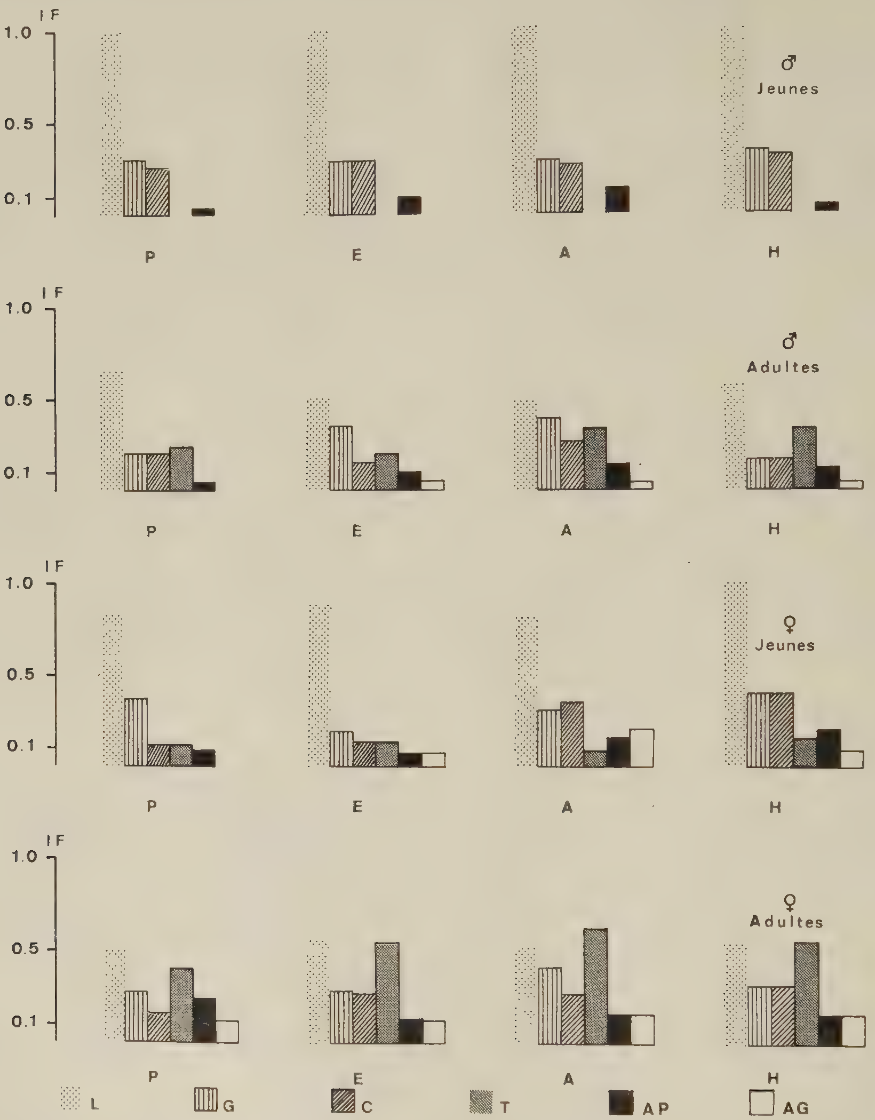

Figure 2. Mise en évidence de l'indice de fréquence (IF) durant les différentes saisons pour les groupes zoologiques trouvés dans les contenus stomacaux, de *Myliobatis aquila*. L: Lamellibranches; G: Gastéropodes; C: Crustacés; T: Téléostéens; AP: Annélides polychètes; AG: Autres groupes.

Discussion

Les observations sur le régime alimentaire de *M. aquila* des côtes tunisiennes correspondent dans l'ensemble aux écrits de la littérature ichthyologique. L'espèce se nourrit d'Invertébrés benthiques (parmi lesquels figurent surtout les Lamellibranches, les Gastéropodes et les Crustacés) et de Téléostéens.

Les jeunes individus des deux sexes se nourriss essentiellement d'Invertébrés benthiques. Les prop tions de Téléostéens ne deviennent importantes c chez les adultes et plus précisément chez les femell Autrement dit au fur et à mesure que les spécim vieillissent et augmentent de taille il apparaît variations qualitatives dans le choix spécifique aliments. L'indice de fréquence des Invertébrés b au 3. Liste et quantités des genres ou espèces identifiées dans les contenus stomacaux de *Myliobatis aquila* en fonction du sexe, de l'âge et des saisons

Sexe	Mâles								Femelles								
Âge	Jeunes				Adultes				Jeunes				Adultes				
Saisons	P	É	A	H	P	É	A	H	P	É	A	H	P	É	A	H	Total
Nombre d'estomaces	39	42	38	44	36	24	29	30	29	44	33	19	30	36	23	27	523
elides polychètes																	
is sp.	1	2	1	–	1	–	–	1	–	–	3	2	1	1	3	1	17
ione hystrix	–	–	1	–	–	1	–	1	–	–	–	–	1	–	–	1	5
odite aculeata	–	–	–	–	–	–	–	–	–	–	1	1	–	1	–	–	3
erminables	–	1	2	2	–	1	3	1	2	2	–	2	3	3	1	2	25
nculiens																	
nculus nudus	–	–	–	–	–	–	–	1	1	–	–	–	–	–	1	1	4
erminables	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	2
éropodes																	
ostoma zizyphinus	1	–	–	–	1	–	1	–	1	–	–	–	–	1	–	–	5
donta turbinata	–	–	1	–	–	–	1	–	1	–	–	–	–	–	–	–	3
a rugosa	1	1	1	–	1	–	–	–	1	–	–	–	1	1	–	–	7
doris maculata	1	–	1	–	–	–	–	–	1	–	–	–	1	1	1	–	6
a hebraea	–	1	1	1	–	–	1	–	–	–	–	–	–	–	–	–	4
a millepunctata	–	–	–	1	–	–	1	–	–	–	–	–	–	1	–	–	3
a sp.	–	–	2	–	–	–	–	–	–	–	–	–	–	–	–	2	4
x trunculus	–	1	–	–	2	2	1	1	1	2	2	3	1	–	2	2	20
x brandaris	–	–	–	–	2	2	1	–	1	2	1	3	1	–	2	2	17
x sp.	–	–	–	2	–	–	–	–	–	2	2	–	–	–	1	2	9
alia erinacea	–	–	–	1	–	1	–	–	–	1	–	–	–	–	–	–	3
nder lignarius	1	–	–	1	–	–	–	–	–	–	1	–	1	1	–	–	5
s leporina	–	–	–	–	2	1	–	–	–	–	–	–	–	1	–	–	4
branchea meckeli	1	1	1	1	–	–	1	–	1	–	1	2	2	–	–	–	11
branches	2	1	–	–	–	–	–	–	1	–	–	–	–	–	1	–	5
erminables	2	4	3	5	–	1	2	3	–	–	1	1	2	3	1	–	28
ibranches																	
ys opercularis	2	1	2	4	2	1	1	–	2	2	3	2	1	1	–	–	24
ys glabra	1	1	2	3	2	–	–	–	1	3	3	1	1	1	–	–	19
ys varius	1	3	2	2	2	–	–	3	1	2	3	1	–	1	–	–	21
ys sp.	7	3	4	3	2	1	2	3	–	3	5	1	1	1	1	1	38
n jacobaeus	2	2	2	4	2	2	2	2	4	2	–	–	–	1	–	–	25
um aculeatum	1	–	–	1	–	2	–	–	–	–	–	–	–	–	–	–	4
um sp.	–	–	2	3	–	–	3	2	–	2	–	–	–	3	–	–	15
s verrucosa	–	–	1	1	–	1	–	–	4	1	2	–	1	–	3	–	14
s decussatus	3	4	2	4	2	3	–	–	–	4	3	2	3	4	2	1	37
na sp.	2	–	1	1	1	–	–	–	–	2	–	–	–	1	–	–	8
ra corallina	–	1	1	1	1	–	–	–	–	1	–	1	–	–	–	1	7
erminables	11	16	14	11	8	5	2	5	10	15	5	8	5	8	4	7	134
alopodes																	
officinalis	–	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1
la rondeleti	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	2
o vulgaris	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1	1	3
tacés																	
la mantis	1	1	–	2	1	1	1	1	1	1	1	–	1	2	1	2	17
squilla eusebia	–	–	–	1	–	–	–	–	–	1	1	–	1	1	–	–	5
us ruber	2	2	1	3	1	–	1	1	1	1	1	1	1	1	1	1	19
a carinata	2	2	1	–	1	–	1	1	1	1	2	–	–	–	2	–	14
or cataphractus	1	2	1	–	1	–	1	1	–	2	1	2	–	–	–	1	13
nassa sp.	1	–	–	–	–	–	–	–	–	1	1	1	–	–	–	–	4
anus arrosor	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	–	2
pe lanata	–	–	2	2	–	1	–	–	–	–	2	1	–	1	–	2	11
cyclus rotundatus	1	–	2	–	1	–	1	–	–	1	1	2	–	–	–	–	9
opipus puber	–	–	1	–	–	–	1	–	–	–	–	–	–	–	–	–	2
opipus tuberculatus	–	–	1	–	–	–	–		–	–	–	–	–	–	–	2	3
plax rhomboides	–	1	1	1	1	–	–	–	–	–	–	–	1	–	–	2	7
us dorsettensis	–	1	–	1	–	–	–	–	–	–	–	–	–	1	–	–	3

Tableau 3. (suite)

Sexe	Mâles								Femelles								
Âge	Jeunes				Adultes				Jeunes				Adultes				
Saisons	P	É	A	H	P	É	A	H	P	É	A	H	P	É	A	H	Tot
Echinodermes																	
Sphaerechinus granularis	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1
Spatangus purpureus	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1
Echinocardium cordatum	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	–	1
Echinaster sepositus	–	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	2
Ophiothrix fragilis	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	2	2
Ophioderma longicauda	–	–	–	–	–	1	–	–	–	–	1	–	–	–	–	1	3
Ascidiacées																	
Halocynthia papillosa	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1	1	3
Microcosmus sulcatus	–	–	–	–	–	–	1	1	–	–	–	–	–	1	1	–	4
Bothryllus schlosseri	–	–	–	–	–	–	1	1	–	–	–	–	–	1	–	–	3
Selaciens																	
Scyliorhinus canicula	–	–	–	–	–	–	–	–	–	–	–	–	–	–	–	1	1
Téléostéens																	
Sardina pilchardus	–	–	–	–	2	2	1	2	–	–	–	–	2	2	–	2	13
Engraulis encrasicholus	–	–	–	–	2	–	–	1	–	–	–	–	2	–	–	2	7
Argentina sphyraena	–	–	–	–	1	–	–	3	–	2	–	–	2	2	–	2	12
Conger conger	–	–	–	–	–	–	–	1	–	–	–		–	1	–	–	2
Merlucius merlucius		–	–	–	–	–	–	1	–	–	–	–	2	1	–	2	6
Paracentropristis hepatus	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1
Cepola rubescens	–	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	1
Mullus sp.	–	–	–	–	–	1	–	–	–	–	–	–	2	–	2	1	6
Maena maena	–	–	–	–	–	1	–	–	–	–	–	–	–	–	1	–	2
Callionymus lyra	–	–	–	–	–	–	1	–	–	1	–	–	–	–	–	1	3
Callionymus phaeton	–	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	2
Blennius ocellaris	–	–	–	–	–	–	–	–	–	–	2	1	–	2	–	2	7
Gobius qucdrimaculatus	–	–	–	–	–	–	–	–	–	–	–	1	–	–	2	1	4
Gobius jozo	–	–	–	–	1	–	1	–	–	–	–	–	1	2	–	1	6
Gobius paganellus	–	–	–	–	–	1	–	–	–	–	–	–	1	2	2	–	6
Gobius sp.	–	–	–	–	–	–	2	–	–	–	–	–	1	2	–	–	5
Lepadogaster gouani	–	–	–	–	1	–	–	–	–	–	–	–	–	–	2	–	3
Solea solea	–	–	–	–	–	–	1	1	–	–	–	–	–	1	1	–	4
Microchirus ocellatus	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1
Monochirus hispidus	–	–	–	–	–	–	1	–	–	–	–	–	–	–	1	–	2
Arnoglossus lanterna	–	–	–	–	–	–	–	–	1	–	–	–	–	–	1	–	2
Citharus macrolepidotus	–	–	–	–	–	–	–	–	2	2	1	–	2	1	2	2	12

thiques diminue chez tous les adultes tandis que celui des Téléostéens augmente considérablement.

Ce phénomène de «changement spécifique des proies préférentielles» n'est pas propre à *M. aquila* mais concerne également d'autres Hypotrêmes.

Du Buit (1968) fait des remarques analogues sur certains Rajidae des côtes françaices de la Manche comme *Raja clavata*, *R. naevus*, *R. montagui*, *R. fullonica*, *R. batis*. Cet auteur écrit: «Les changements de nourriture observés en cours de croissance ne sont pas imposés par un changement d'habitat ... Ils sont simplement dus à l'augmentation de la taille des individus ...»

Holden et Tucker (1974) réalisent des observations identiques sur quelques Raies des mers britanniques: «In general, the stomach contents of *R. clavata*, *R. montagui* and *R. naevus* reflect the increasing abili of the larger fish to catch more active prey».

Enfin en Méditerranée, sur la bordure yougosla de l'Adriatique Jardas (1972) note à propos de *clavata*: «The contents of the food changes deper ing on the size of the fish. The importance of Schiz poda in the nourishment decreases with the grow of the fish and then other animal groups are progr sively introduced. Fish in the food come the latest

Le long des côtes tunisiennes nous avons fait mêmes constatations sur deux Raies communes da le golfe de Tunis: *Raja miraletus* et *R. radula* (Capa et Azouz, 1975).

Pour *Myliobatis aquila* l'indice de fréquence Téléostéens plus élevé chez les adultes peut s'expliq non seulement par une plus grande habileté dans

re des proies mais aussi par la vie semi-péla-
que mènent les grands exemplaires. Ceux-ci
uivent les bancs de Poissons migrateurs et plus
ulièrement les Clupeidae. Nous avons trouvé à
urs reprises des espèces faisant partie de cette
e dans les contenus gastriques de nombreux
uila.

Conclusion

batis aquila est une espèce vorace qui se nour-
ondamment toute l'année.

groupes zoologiques préférentiels consommés
Sélacien sont en majorité des Invertébrés ben-
es pour lesquelles il ne semble pas réaliser de
spécifique. La part de plus en plus importante
éléostéens dans les contenus stomacaux de *M.*
se fait avec l'accroissement de taille. Ce phé-
e étant beaucoup plus marqué chez les femelles
teignent en général une taille plus importante
z les mâles.

il faut tenir compte chez les grands individus
aquila du passage de la vie benthique à la vie
élagique qui modifie leur comportement et les oriente vers la capture d'animaux ayant un mode de vie analogue.

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Fishing power, fishing effort, density, fishing intensity and fishing mortality

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This paper derives relationships between fishing power, fishing effort, density, fishing intensity and fishing mortality. Fishing power is defined as the product of the area of influence of the gear during a unit operation and the efficiency of the gear during that operation. As a consequence of its definition it is shown that fishing power is the effective area covered by the gear during a unit operation. Fishing effort is defined as the product of fishing power and the number of unit operations and is therefore the total effective area covered by the gear during a number of unit operations. Consequently catch per unit effort is a direct measure of the density of the fish. Fishing intensity is defined as the fishing effort per unit area per unit time and hence is equal to the effective area covered by the gear per unit time as a fraction of the area occupied by the stock. It also shows that fishing intensity is the fraction of the fish which are caught per unit time provided certain requirements underlying the theory are well met.

Fishing mortality is defined as the fraction of the fish caught per unit time from which it follows that when the requirements referred to above are satisfied fishing mortality is also equal to fishing intensity. Fishing power is difficult to measure and therefore the concept of relative fishing power as a measurable quantity is introduced. This leads to a discussion of relative fishing effort, relative density and relative fishing intensity. Relative fishing intensity is proportional to fishing mortality and as such can be used to record changes in fishing mortality. Furthermore, if the constant of proportionality, the catchability coefficient, is measured, the relative fishing intensity can be used for direct estimation of fishing mortality.

Introduction

It is often found that even when vessels fish together on the same density of fish their catches per fishing time vary. This discrepancy, as distinct from normal random fluctuations, can be attributed to the differences in fishing power between vessels. Hence whenever vessel statistics are being used for measuring fish abundance some correction should be made for this variation. The types of corrections which can be made are presented in this paper along with an explanation of the interrelationships between fishing power, fishing effort, density, fishing intensity and fishing mortality.

Fishing Power

The fishing power of a particular gear is defined (Gulland, 1969) as the product of the area of influence of the gear during a unit fishing operation and its efficiency during that operation. That is,

$$r = a\frac{c}{n}$$

where r is the fishing power
a is the area of influence of the gear for
unit operation
c is the number of fish caught during a u
operation
n is the number of fish within the area a duri
the unit operation

and $\frac{c}{n} = p$, is the efficiency of the gear for t
unit operation.

In practice, when we consider the operations o
given vessel for which a, c and n are known for ea
of g unit operations, then the mean fishing po
for that vessel would be estimated by

$$\bar{r} = \frac{\Sigma ap}{g}$$

The area of influence of the gear is obviou
dependent on the quantity and size of the gear,

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and its mode of operation. The same is true of
iciency, which is also dependent on the avail-
y and behaviour of the fish within the area of
nce of the gear.

we assume that,
e efficiency of the gear is independent of the
mber of units of gear used during a particular
hing operation,
e efficiency of the gear is independent of the
nsity of fish,
e availability and behaviour of the fish within
e area of influence of the gear remains constant,
e unit operation is chosen so that within the
nits of practicability, the area of influence of
e gear remains constant for a vessel,

each vessel will have a unique fishing power
will remain so as long as the gear and its
of operation remains constant.
the situation where assumptions 1, 2 and 3 are
d a vessel will have different efficiencies depend-
the number of gear units on the vessel, the
ty of fish and the behaviour of the fish, and it
necessary to determine the fishing power of
ssel relevant to all of these situations.
more closely the unit operation is associated
the operation of the gear, the more reasonable
urth assumption becomes. For example, in the
a trawl fishery, a boat year, a day fishing and
ur with the net at the bottom are progressively
choices of a unit operation.
hough the fishing power of a gear is defined
product of the area of influence during a unit
tion and the efficiency of the gear, it is most
niently measured as the product of catch per
peration and the reciprocal of density. That is,
e relationship

$$r = c/d \; (= a\,c/n)$$

e d is the density of fish in the area of influence
e gear during the unit operation. The catch per
operation is obviously easy to measure and in
ed instances it is possible to measure the density
h.

Relative Fishing Power

he fishing power of a given gear cannot be
ured and it is necessary to consider the relative
g power, r', where r is related to r' by the
onship

$$r = qr'$$

alled the catchability coefficient and has a range
lues depending on the choice of units for r'.

Relative fishing power provides a convenient means of comparing vessels and can be measured in several ways (Gulland, 1956; Robson, 1966). Three examples of how it can be used to compare vessels are given below.

1. If we consider a given vessel fishing on a given density of fish for which c is known for each of g unit operations, then the mean relative fishing power for that vessel is

$$\bar{r}' = \frac{\Sigma c}{g}$$

   and as a consequence of this definition $q = 1/D$ where D is the density of fish in the area being fished.
   Thus when a number of vessels operate together on a common density of fish it is possible to use the mean catch per unit operation to compare the fishing power of the vessels.
2. It is more usual, however, for vessels to operate on areas of different densities and at different times. In this case it is necessary to compare their fishing powers by reference to a standard vessel. That is, for the i^{th} vessel fishing alongside the standard vessel (denoted by subscript s) in the same area

$$\bar{r}'_i = \left(\frac{\Sigma c_i}{g_i}\right) \Big/ \left(\frac{\Sigma c_s}{g_s}\right)$$

   In this situation $q = r_s$
   This approach can be extended to vessels which have not fished alongside the standard vessel provided they have fished alongside vessel(s) which in turn can be calibrated against the standard.
3. If it can be established that relative fishing power is proportional to a function of a gear characteristic, it follows that fishing power is also proportional, in which case

$$\bar{r}' = f(G)$$

   where $f(G)$ is a function of the gear characteristic. In this situation q has a number of values depending on the form of the function.

Some gear characteristics which have been shown to be related to fishing power are vessel length, tonnage and horsepower, dredge width and number of hooks.

Fishing Effort

The effort, X, of a vessel during any period of time is the product of its fishing power and the number of unit operations expended during that period; so for a given vessel.

$$X = \bar{r}g$$

From its definition it can be seen that fishing power is the effective area covered per unit operation. Similarly it can be seen that fishing effort is the sum of the effective areas covered during g unit operations.

Relative Fishing Effort

The relative fishing effort, X', for a given vessel is

$$X' = \bar{r}'g$$

Substitution yields $X' = \bar{r}g/q = X/q$
That is, the relative effort is proportional to the real effort with $1/q$ being the constant of proportionality.

Density

The density of fish in a given area is the number of fish per unit area. If we assume that the distribution of fish over the area is uniform, then the catch per unit fishing effort of a vessel or of the whole fleet provides the density of the fish in that area. That is,

$$D = C/X$$

where D is the density estimated as a result of the fishing activities and C is the catch made during X units of fishing effort.

Relative Density

The catch per unit relative fishing effort, C/X', is not equal to density because X' is not equal to X, and hence is not the mean effective area covered. It does however allow the comparison of densities, since

$$D' = C/X'$$

where D' is the relative density indicated by the fishing of a given vessel. Substitution gives

$$D' = qC/X = qD$$

That is, the relative density is proportional to the absolute density with q being the constant of proportionality.

Fishing Intensity

Fishing intensity, f, is defined as the fishing effort per unit area per unit time; for a given vessel,

$$f = \frac{X}{A} \Big/ t$$

where A is the area occupied by that portion of stoc
under consideration, and
t is the time interval for X units of fishin
effort.

From its definition it can be seen that fishing in tensity is the effective area covered per unit tim during fishing operations as a fraction of the are occupied by the stock.

If redistribution of the fish occurs between eac unit operation, and the density of the stock in th area is uniform, then f is also the fraction of th available fish caught by the vessel per unit time That is, after substituting for X in the above equatio

$$f = \frac{C}{D}\,\frac{1}{At} = \frac{C}{N} \Big/ t$$

where N is the number of fish.

If complete redistribution does not occur betwee each unit operation, then the next unit operation o exactly the same area results in f being an over estimate of the fraction of the available fish caugh per unit time, while the next unit operation on different area results in f being an underestimate this fraction. If fishing is randomly conducted withi the area these errors are minimised.

In the situation where the fish are not uniforml distributed within the area the proportion of th stock number taken during each unit operation w not be constant across the fishing grounds, but wi depend on the local density of the fish. Units effort applied where the density is high will cause greater proportional mortality than those where t density is low. In such a situation it is necessary divide the total area into areas of roughly unifor density and analyse the data for these sub-are separately.

In this case to obtain the mean fishing intensity m vessels operating in x areas, the effort in each ar must be weighted by the density of fish in the are The mean fishing intensity applied by the m boa over the x areas becomes

$$\bar{f} = \sum_{j=1}^{x} \left(\bar{D}_j X_{\cdot j}\right) \Big/ \left(\sum_{j=1}^{x} \bar{D}_j A_j\right) t$$

where D_j is the estimated mean density in the area during the time interval, t.

Alternatively the mean fishing intensity can obtained by weighting the fishing intensities in ea area by the number of fish in the area, that is

$$\bar{f} = \sum_{j=1}^{x} \left(\bar{N}_j f_{\cdot j}\right) \Big/ \left(\sum_{j=1}^{x} \bar{N}_j\right)$$

e $\bar{N}_j$ is the estimated number of fish in the j^{th} during the time interval.

both cases rearrangement gives

$$\bar{f} = \sum_{j=1}^{x}\left[\left(C_{\cdot j}/X_{\cdot j}\right)X_{\cdot j}\right]\Big/\left(\sum_{j=1}^{x}\bar{N}_j\right)t$$

$$= \left(\sum_{=1}^{x} C_j/\bar{N}_j\right)\Big/ t$$

h is the fraction of the mean stock occupying areas caught by the m vessels per unit time.

mean fishing intensity for a given area can be puted in the same way for a time when the dens- r number of fish changes. That is, the fishing or fishing intensity for each short time interval ng which stock abundance is reasonably constant ighted by the mean density or mean number of espectively.

Relative Fishing Intensity

relative fishing intensity for a given vessel is

$$f' = \frac{X'}{At}$$

e f' is the relative fishing intensity.

tution gives

$$f' = \frac{X}{qAt} = \frac{f}{q}$$

is, the relative fishing intensity is proportional he real fishing intensity with $1/q$ being the con- t of proportionality.

s before when computing the mean relative fish- intensity over either time or space the relative ng effort in each time interval or sub-area must eighted by the density (or some index of density) lternatively the relative fishing intensity in each interval or sub-area must be weighted by the bers (or some index of numbers).

Fishing Mortality

fishing mortality, F, associated with the use of a icular gear is the fraction of the available fish ght per unit time (Beverton and Holt, 1954). t is,

$$F = \frac{1}{N}\frac{dC}{dt}$$

Earlier it was shown that fishing intensity is given by

$$f = \frac{C}{N}\Big/ t$$

when the density of the stock under consideration is uniform and complete redistribution of the fish occurs after each unit operation (or fishing is random). When considered over a small time interval the above equation reduces to

$$f = \frac{1}{N}\frac{dC}{dt}$$

It follows then that $F = f$.

In practice when we consider fishing taking place over some finite time period or across sub-areas in which the fishing mortality or numbers of fish may vary, it is necessary to consider a mean fishing mortality. This is computed in a similar way to mean fishing intensity by weighting the individual fishing mortalities by the number of fish present (or some index of numbers). That is,

$$\bar{F} = \frac{\int FNdt}{\int Ndt} = \frac{\int dC}{\int Ndt} = \frac{C}{N}\Big/ t = \bar{f}$$

Again it can be seen that fishing mortality and fishing intensity are identical.

It follows that if $F = f$ then $F = qf'$. That is, fishing mortality is proportional to relative fishing intensity with q being the constant of proportionality. This relationship is commonly used to allow estimation of q when F and f' are obtained independently.

Discussion

The statistics provided by fishing vessel activity are invaluable for estimating fish abundances, densities and mortalities provided that certain requirements underlying the theory are satisfied.

It is important to remember, for example, that the fishing power of a vessel may not always remain constant. If the vulnerability of the fish changes, or if the fishing grounds become progressively saturated with gear so that the gear units interfere with each other, or if the gear tends to lose its efficiency by being saturated with fish, the fishing power will change and these changes will need to be recognised and measured.

It is also important that in the area and time interval under consideration the density of fish is uniform, otherwise incorrect estimates of density from catch per unit effort and fishing mortality from fishing intensity may arise. The common method of satisfying this requirement is to group the data over small statistical areas and time units. If fishing is random it may be possible to relax this requirement; this is also true of the requirement that redistribution of the fish must occur between fishing operations if fishing mortality is to be estimated correctly from fishing intensity.

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Codworm – a possible biological indicator of the degree of mixing of Greenland and Iceland cod stocks

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During a quantitative survey of the infestation of North Atlantic cod stocks with larvae of the codworm, *Terranova decipiens* Krabbe, considerable differences between the infestations of the various populations were observed. In particular, larvae were virtually absent from cod at Greenland and abundant in those at Iceland. However, on the spawning grounds off southwest Iceland, a reduction in the characteristic level of infestation of Iceland cod was noted. This was thought to be due to the immigration of uninfested cod from Greenland waters. An examination of the infestation in relation to the age of the host further supported this theory. The evidence suggests that the relative abundance of codworm might be used as a biological indicator, providing an aid to the determination of the relative proportions of Iceland and Greenland components of the cod population on the spawning grounds at southwest Iceland.

Introduction

e codworm, *Terranova decipiens* Krabbe, 1878, is anisakine nematode, parasitic as an adult in the machs of pinnipeds, especially the Grey seal, *ichoerus grypus* (Young, 1972). The life cycle of nematode, summarized in Figure 1, includes a al stage which is encysted in the flesh of a demer- fish. Because of consumer reaction and the pos- e pathogenic effects of the worm on man (Suzuki l., 1972; Little and MacPhail, 1972), there has n increasing concern about the occurrence of cod- rm larvae in the cod, *Gadus morhua*. In order to ntify and improve our knowledge of the incidence this nematode, a survey of the North Atlantic l Arctic cod stocks was undertaken by the former heries Helminthology Unit. During this survey, siderable geographical variation in the *T. decipiens* station was observed (Platt, 1975). The variation nfestation within the cod stocks occurring in Ice- d and Greenland waters is of particular interest. uantitative studies of the parasite fauna of marine have increasingly shown differences between inct stocks of several species, and may be parti- rly useful as natural biological indicators of fish migrations and the mixing of stocks. Previous workers have suggested several criteria which should ideally be met before a parasite may be considered suitable as a biological indicator (Kabata, 1963; Sindermann, 1961). These may be summarized as follows:

1. The parasite should be common in one population of the studied host species and rare or absent in another.
2. The infestation should be of reasonably long duration, at least several years.
3. The parasite should not bring about the death of its host.
4. The incidence of the parasite should remain relatively stable during the period of the study.
5. The parasite should preferably include in its life cycle only that host species which is being studied.
6. The environmental conditions in the areas studied should be within the physiological range of the parasite.

However, not all of these criteria can consistently be fulfilled in real situations.

The only criterion not satisfied by the codworm infestation in the Greenland and Iceland cod stocks is that the parasite should include in its life cycle only that host species which is being studied. As Kabata (1963) explained, this does not preclude the

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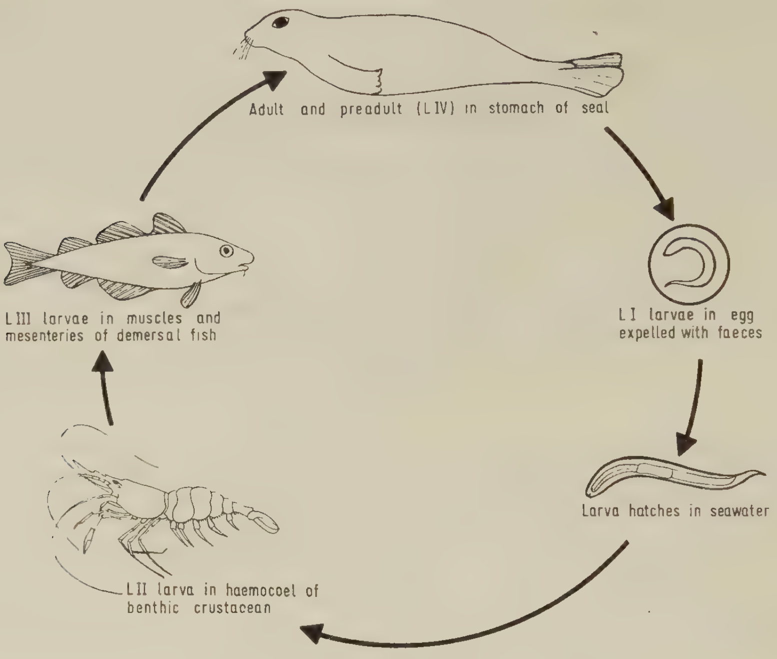
Adult and preadult (L IV) in stomach of seal
L I larvae in egg expelled with faeces
Larva hatches in seawater
L II larva in haemocoel of benthic crustacean
L III larvae in muscles and mesenteries of demersal fish

Figure 1. The life cycle of *Terranova decipiens.*

use of the parasite as a biological tag. He remarks that parasites with complex life cycles require wider study than those with single life cycles, because the occurrence and abundance of a parasite depends on the distribution and abundance of the populations of all its hosts. However, the first criterion requires that the parasite should be rare or absent in one of the host populations being studied, and this should essentially be the case for satisfactory quantitative work on the host populations. In order to satisfy this condition it may be necessary for one or both of the last two criteria to remain unfulfilled since the absence of a parasite in a host population suggests that there is a break in the life cycle through one cause or another.

Migration studies have shown that a component of the spawning population of cod on the Icelandic spawning grounds is of Greenland origin (Harden Jones, 1968). These fish are thought to be recruited to the Iceland stock after spawning (Anon, 1973). The nematode survey revealed that codworm was virtually absent from cod at Greenland, but abundant in those from Iceland waters. However, the infestation of cod in the region of the spawning grounds off the southwest coast of Iceland (area 3, Fig. 2) was significantly less than in any other region at Iceland. It was thought that this lower infestation might result from the immigration of an uninfested component of mature cod from Greenland to spawn a Iceland. If this is the case, comparison of the degre of infestation of the various groups of cod may pro vide an additional means of quantifying the propor tion of Iceland to Greenland cod on the spawnin grounds off southwest Iceland. Thus, a further ana lysis of the data obtained during the survey was under taken, special emphasis being placed on changes i the degree of infestation with increasing age of th cod.

Methods

Approximately 3100 cod, taken from Iceland ar Greenland waters, were examined between 1 Febru ary 1971 and 30 April 1973. Samples were obtaine from the landings of the British distant water trawlin fleets of Fleetwood, Grimsby and Hull, during r search cruises of the Ministry of Agriculture, Fis eries and Food's RV "Cirolana", and during cruise of a research vessel of the Icelandic Mari Research Institute, Reykjavik.

Those samples which were obtained from com mercial landings consisted of 30 to 65 kg of cod ar codling. The fish were packed in crushed ice ar sent to the laboratory overnight by road. T grounds from which the fish were taken were dete

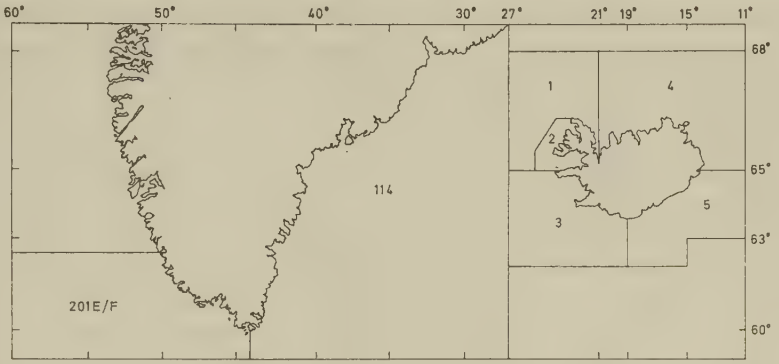

Figure 2. The geographical areas sampled during the survey.

ned by interview and samples obtained from a sel which had trawled in more than one area were luded from the analysis of the data. The samples en during research cruises were either examined board or deep frozen and examined on return to laboratory.

The total length of each fish was measured to the timetre below and its weight determined to the rest 50 g. The sagittal otoliths were removed for determination. For the purpose of determining ir age, fish were assumed to have been spawned 1 January.

he cod were filleted and each fillet divided into portions, the *flap*, that part of the flesh which rounds the body cavity, and the *fillet*, the remnder of the body musculature. Each portion was mined by slicing the flesh over a candling table d with four 20 watt fluorescent light tubes, ducing an intensity of 75 foot candles at the rking surface. The number and identity of the matodes found in each portion was recorded. At t, the identification was checked by microscopic mination, the worms having been killed and fixed hot 70% alcohol or cold glacial acetic acid, preved in 70% alcohol and cleared in lactophenol rland, 1961). Later, they were identified by eye ne, microscopic examination being used only when re was any doubt. The descriptions in Berland 6) and Grainger (1959) were used as an aid to ntification.

Results

The distribution of sampling is shown in Table 1. It has been suggested that the East Greenland and South-west Greenland (ICNAF Division 1E–F) cod may be considered a single stock, based on the results of tagging experiments (Anon, 1973). Thus the data from these areas have been grouped and are given in Table 2. Of the 364 cod examined from Greenland waters only five fish, of which two were of mature age, were found to be infested with *Terranova decipiens* larvae.

The degree of infestation of Iceland cod with *T. decipiens* larvae, recorded as the percentage of cod infested within each age class, is shown in Figure 3. In view of the seasonal variation in fishing between the grounds around Iceland, it has not been possible

Table 1. The distribution of sampling

Geographical Area (see Fig. 2)	Number of fish examined
East Greenland 114	83
South-west Greenland 201 E/F	281
Iceland 1	831
Iceland 2	297
Iceland 3	294
Iceland 4	828
Iceland 5	482

le 2. The degree of infestation of cod with *Terranova decipiens* larvae in Greenland waters

e	2	3	4	5	6	7	8	9	10	11	12	13	14
. examined	4	3	39	33	29	24	86	96	31	13	3	1	2
. infested	0	0	1	0	2	0	1	1	0	0	0	0	0

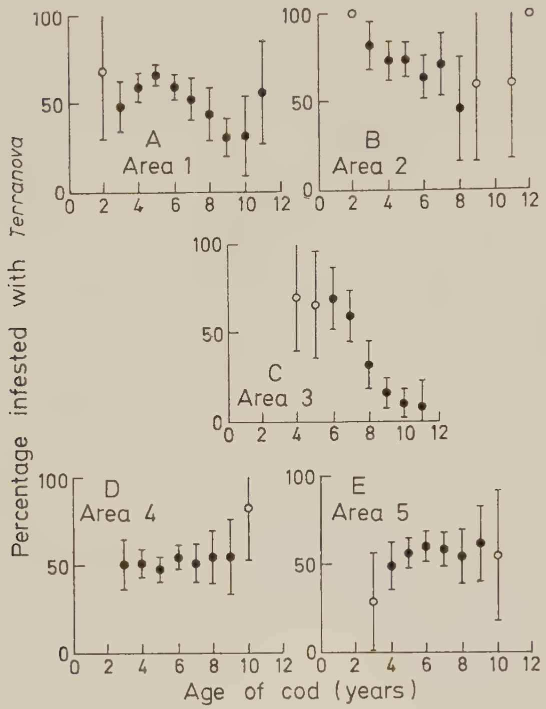

Figure 3. The variation in *Terranova decipiens* infestation of cod in Icelandic waters with increasing age of the host. ○, 5 to 10 cod in age class sample; ●, more than 10 cod in age class sample. The 95% confidence limits are shown.

to sample every area in each season of the year. Thus the data presented in Figure 3 are the sum of the results obtained from Icelandic waters during the whole sampling period.

It will be seen from Figure 3 that the relationship between the proportion of cod infested and the age of the host differs in the areas studied. Cod from areas 4 and 5 (Fig. 2) have similar infestations which gradually increase with the age of the host from around 45% at age 3 years to 60% at 9 years. The infestation of cod in area 2, in the region of Breidafjordur, is the greatest. Between 60% and 80% of the fish from this area were infested and the infestation appears to fall gradually with increasing age to a level similar to that observed in areas 4 and 5, though there were really insufficient examples of older fish for a general statement about their degree of infestation to be made, a point borne out by the great range of the 95% confidence limits (Fig. 3B). The infestation of cod from areas 1 and 3 increases with age in the younger fish, but at about 7 years of age this increase in the proportion of the population infested with codworm is reversed and, particularly in fish from area 3, the region of the spawnir grounds to the southwest of Iceland, there is a shar drop in the degree of infestation (Fig. 3C).

Discussion

In view of the present knowledge of spawning migr tions of cod in Greenland and Iceland waters (Harde Jones, 1968), the rapid fall in the level of *Terrano* *decipiens* infestation observed in mature cod on tl spawning grounds off southwest Iceland migl reasonably be expected to be caused by the immigr tion of uninfested mature cod from Greenland. Th the majority of the specimens obtained from tl area were obtained during the spawning period len further support to this interpretation. These imm grants are believed to be recruited to the Icela cod stock (Anon, 1973) and can be expected to mo with the native cod population to feeding groun on the Icelandic continental shelf. An examinati of the *T. decipiens* infestation of cod from the nort west of Iceland, area 1, revealed a relationship wi age which reflects the rapid fall in infestation whi was observed in the older cod on the spawni grounds, but is not quite so extreme. This observ tion further supports the idea that Greenland c are recruited to the Icelandic stock and, as the majo ity of specimens were obtained from the area duri the three months immediately following the spawni season, further suggests that the post-spawning r covery grounds are located in this area. That t degree of infestation of the older age classes w greater than on the spawning grounds indicates tl the previously uninfested Greenland component the stock is now exposed to infestation by *T. decipi* whilst feeding. It is not known how long it will ta for this Greenland component to attain the infes tion levels of the native component as the sampli effort was necessarily seasonal and insufficient f were obtained from this area during the win months.

The situation observed in area 2, off Breidafjord is rather anomalous since it also happens to be region in which the main breeding concentrations Grey seals, the definitive hosts to *T. decipiens*, located (Smith, 1966). Thus as one might exp the infestation of cod in this area is greater than el where at Iceland. This is particularly evident in case of the younger fish, where there is a sligl greater degree of infestation than in older cod. I likely that these immature fish do not move far fr their feeding grounds, thus allowing the infestat to build up in this section of the population. T mature fish, however, will tend to mix with th le 3. The proportion of Iceland to Greenland cod on the spawning grounds off south-west Iceland. The numbers of fish examined are in parentheses

Age class (years)	% Cod infested at Greenland	at Iceland Area 4 & 5	on spawning ground	Percentage origin of cod Iceland	Greenland
....	1·16 (86)	55·17 (87)	31·82 (44)	57%	43%
....	1·04 (96)	58·54 (41)	16·46 (79)	27%	73%
....	0 (31)	69·23 (13)	11·11 (63)	16%	84%
....	0 (13)	– (1)	8·33 (12)	–	–

n other areas during their migrations and their stations will consequently tend to become re- sentative of the stock as a whole.

n addition to a qualitative description of the wning migration of cod from Greenland to south- t Iceland and its subsequent recruitment to the and stock, a quantitative estimation of the cod- m infestations of the various components of the wning stock should enable the proportions of and and Greenland cod on the spawning grounds be determined. This calculation is based on the el of infestation of each component stock, deter- ned by examining fish in their home waters, and he change in the level of infestation when they mix the Icelandic spawning ground. Jamieson and sson (1971), who studied haemoglobin types in blood, suggest that the genetic composition of spawning population at southwest Iceland nges throughout the season, presumably due to k movements. They also suggest that a mosaic ct of genetic isolates is demonstrable within the wning stock. Thus, when sampling the spawning ulation, a far greater geographical and temporal erage than was possible during this survey would required for an accurate assessment of the com- ition of the spawning cod population. However, h the reservations that the samples of the spawning ery were small and gave neither adequate temporal geographical coverage, the proportions of mature l of Iceland and Greenland origin were determined age classes 8, 9 and 10 years (Table 3). It is im- diately apparent that these proportions are of a y different order to those calculated by the ICES rth Western working group in 1970 using data ained from an examination of otolith types, ristic characters and tagging experiments (Anon, 71). However, it is believed that the use of cod- rm infestation as a biological indicator would be valuable aid to the assessment of the inter-rela- nships of the cod populations at Iceland and eenland.

Acknowledgements

I am grateful to all those who have assisted in obtaining my samples, often under difficult and sometimes hazardous conditions.

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Echo-traces from the North-eastern Atlantic

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Numerous echo-traces produced by biological targets within a depth range of 36–460 m were recorded during cruises by RRS "Discovery II" and RRS "Discovery" in the North-eastern Atlantic ocean. The NIO Precision Echo-Sounder Mk. II was operated at a frequency of 10 kHz. The pulse length was usually set at 2·0 ms. Gain settings were variable. Traces under discussion were obtained between latitudes 16°30′N and 60°N and extended to a maximum longitude of 25°30′W. Fish and cetaceans were thought to be the principal sound scatterers. Various types of trace were recorded. These included weak diffuse continuous layer-traces and also stronger discontinuous layer-traces. Discrete traces from single and aggregated targets were widespread and often in the form of crescent and comet-type echoes. Discrete vertically elongated traces were sometimes encountered. Vertical diurnal migration was often apparent. The complexity of the scattering varied regionally, seeming to depend on the type, density and behaviour of targets. Weak diffuse scattering was widespread. Complexity in strength and type of echoes increased particularly over shallow water. Some of the more interesting traces from various regions of the North-eastern Atlantic are reproduced and discussed.

Introduction

The basic types of echo-trace recordable from biological targets have been summarized by Cushing (1957, 1963, 1973). Fish are thought to be the principal midwater sound scatterers throughout a wide frequency range. Other detectable targets include cetaceans. Most planktonic organisms do not seem to be detectable at relatively low frequencies.

The intensity and type of trace depends not only on sound frequency but also on beam angle, gain setting, ship speed and recording speed. Other factors of major importance include the horizontal and vertical distribution and behaviour of biological targets.

Throughout the last 12 years or so scattering of considerable biological interest has been recorded in the North-eastern Atlantic during cruises by RRS "Discovery II" and RRS "Discovery" in the course of general oceanographic investigations. Many of the traces have been collectively analysed and a quantitative assessment of scattering made, the results of which were discussed previously (Hargreaves, 1975). The object of this paper is to describe and reproduce some of the more interesting traces. The photographs shown are of parts of the original records.

Material and methods

Echo surveys were carried out at various times
the year in the North-eastern Atlantic between Lat
tudes 12° and 62°N and from the European an
North-West African coast to a longitude of a
proximately 28°W. The National Institute of Ocean
graphy multiple phase precision echo sounder Mk.
was operated throughout at a frequency of 10 kH
Sound is emitted into a beam approximately 28°
the –3 dB point, and the transducer introduces

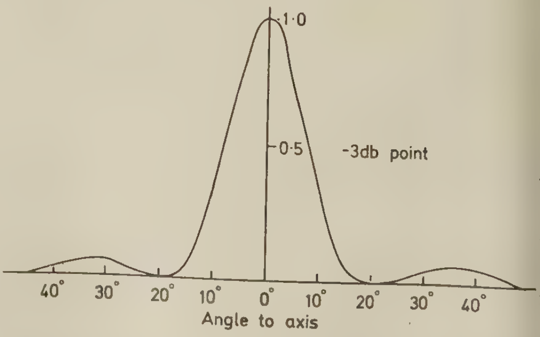


Figure 1. Beam pattern of NIO precision echo sound
Mk. II showing the power at different angles relative
that on the axis.

lar beam shape on reception so that the overall
ctionable response is according to Figure 1.
re are no automatic or time varied gain controls.
argets recordable with this apparatus include
ll fish and some planktonic organisms capable of
nance at low frequencies such as the siphono-
res. Larger non-resonating targets such as fish
cetaceans are easily detected. However, non-
nating plankton is unlikely to be recordable at
frequency (McCartney, in prep.). The effective
ge for the detection of biological targets lies from
roximately 36 to 460 m Near-surface reverbera-
may occur above 36 m. Organisms at depths
ter than 460 m are sometimes, but not often,
cted with the apparatus.

he gain settings were variable but during most
ses were set at a constant moderate level. The
e length which governs the minimum vertical
kness of an echo could be varied between 0·7 ms
5·0 ms but during most transmissions was set at
ms. The echoes were recorded on moist paper
ther with calibrations for depth and time. The
tinuous horizontal lines are spaced at 36 m inter-
, and the vertical lines at 5 min intervals.

pes of trace usually obtained with echo-sounding
aratus have been described by Cushing (1957,
, 1973). These include weak and diffuse con-
ous layer traces caused by evenly but widely
ibuted non-shoaling individuals of relatively low
et strength; dense continuous layer traces from
e closely aggregated and possibly stronger tar-
: and discrete echoes from individuals and isolat-
hoals of high target strength. Often the discrete
es from targets smaller than the width of the
nd cone appear as hyperbolic (or comet-type)
es due to the fact that the distance between the
nd source and a target is maximal if the latter is
r the periphery of the beam, and minimal if it
pens to be present near the centre. In extreme
s the comet shapes are expanded giving elongated
s'. The horizontal extent of an echo varies de-
ding on the position of a target, speed of ship,
recording speed. The vertical extent largely
ends on shoal size and configuration. With the
Hz NIO sounder, traces from single fish of high
strength usually appear as hyperbolic echoes
nstant minimum vertical thickness usually of
m (fingernail traces) or as minute spots. A very
ll shoal of 3–4 fish may produce a hyperbolic
e the vertical thickness of which is slightly greater
that of the 'fingernail' trace. A larger discrete
al may produce a comet-type echo the vertical
kness of which can range from approximately
27 m. Extremely vertically elongated echoes are
ned 'plumes' or 'towers'. The depths of the mid-

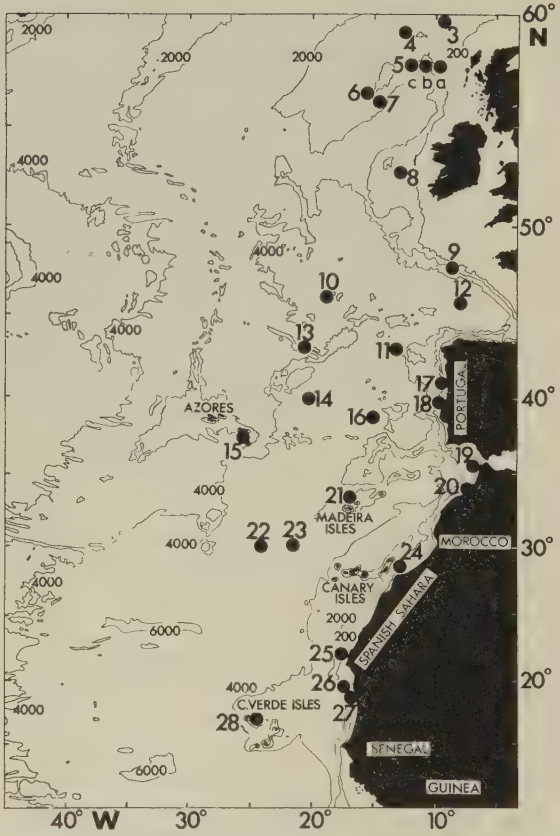


Figure 2. Chart of the North-eastern Atlantic to show positions of echo-traces shown in Figures 3 to 28. Principal depth contours are shown in metres.

water targets which happen to lie close to the centre of the sound cone should be accurately recorded. The depth of those near the periphery of the beam may be over-estimated by up to 10%. Due to the multiple phase recording system, the sea floor may occasionally appear on the record at the same level or above the acoustic scattering when it is actually one or more phases deeper.

Results

The basic types of scattering recorded during the "Discovery" cruises have been summarized previously (Hargreaves, 1975). They were broadly divisible into weak but wide-spread, fine-grain continuous scattering layers probably due to non-shoaling single fish of low target strength; denser discontinuous layers probably from more closely aggregated fish; 'spot' and, 'fingernail' traces from single targets, and

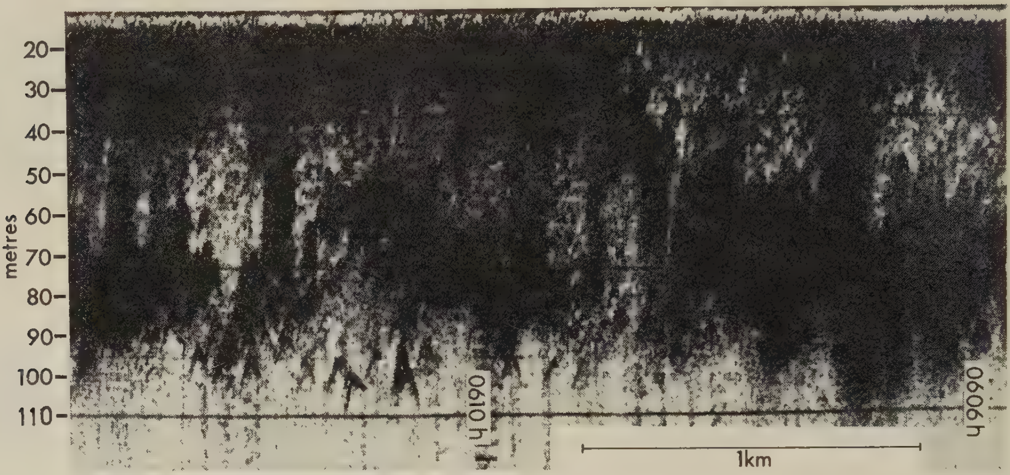


Figure 3. Vertical scale 2 to 124 m. Trace recorded at a position of approximately 59°47′N 9°27′W in early mornin June 1967. Large dense discrete echoes from shoals are seen within the surface 110 m amid lighter more diffu scattering. Small hyperbolae are seen to the left near the bottom of the picture. Relative gain, max – 6 dB; ship spe 12 knots; sea floor at 1232 m; sea surface temperature 11·0°C; wind force 4; mean wave height 0·6 m; sunrise 03·00 moonrise 06·52 h; age moon 4 days.

also larger plumes, towers and comet-traces from fish and cetacean shoals.

Weaker diffuse scattering layers, 'fingernail' traces and minute spots will be referred to as general scattering where appropriate. The 'fingernail' and 'spot' traces were usually apparent within the surface 110 m or so and often appeared more diffuse with increasing depth. This was partially due to the type of echo display employed (McCartney, personal communication) and possibly due to a reduction the signal strength of the targets.

Generally the type of trace recorded in the Nort east Atlantic was found to vary depending on ge graphical location. Those recorded over deep ocean water were moderately variable depending on latitu but were relatively consistent within a given regio A greater amount of variation was encountered coastal water. The chart shown in Figure 2 sho

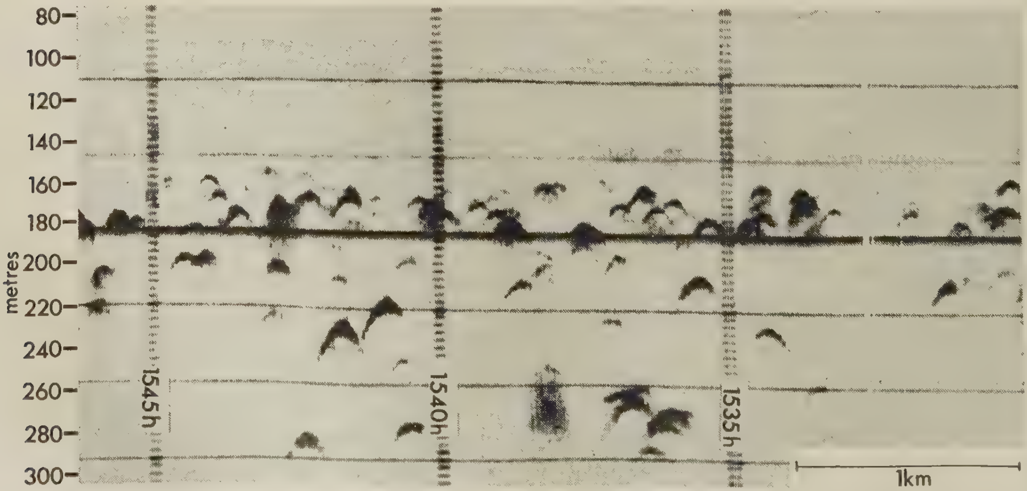
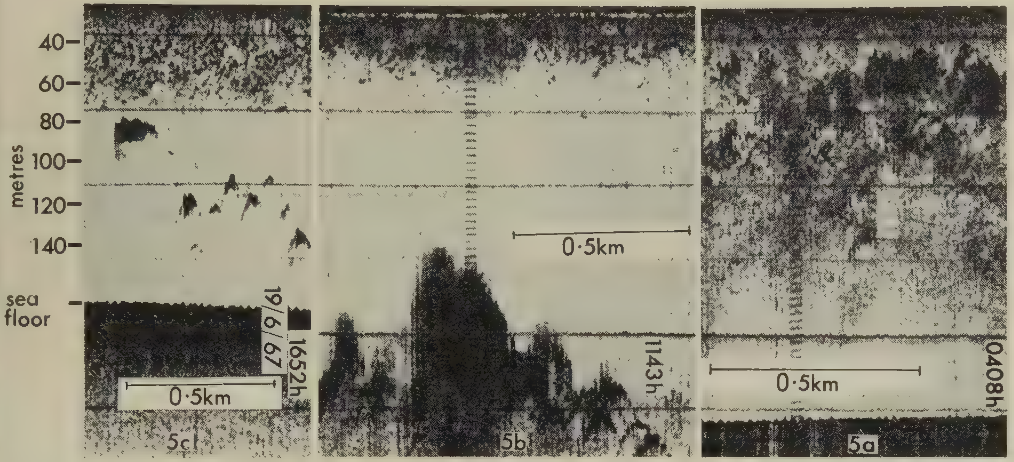


Figure 4. Vertical scale 73 to 303 m. Hyperbolae recorded in mid-water in late afternoon in June 1967 at about 59°50 12°15′W. Each of these echoes is probably due to a small shoal of blue whiting which are common to the area (Bail 1971). Ship speed 8 knots; relative gain max –12 dB; sea floor at 1232 m; sea surface temperature 12·2°C; wi calm; sea calm; sunset 21·14 h; moonrise 23·57 h; age moon 18 days.



ure 5. Vertical scale 25 to 245 m. Extracts from a continuous trace recorded throughout the day on 19 June 1967 g an easterly – westerly transect at approximately 58°45′N. Much of the scattering may be due to blue whiting. tive gain max −6 dB., sea floor at 1630 to 1800 m; sea surface temperature 10·5–11·0°C; wind force 6; mean height 3·3 m; sunrise 02·57 h; sunset 21·06 h; moonrise 17·00 h; moonset 01·50 h; age of moon 11 days.

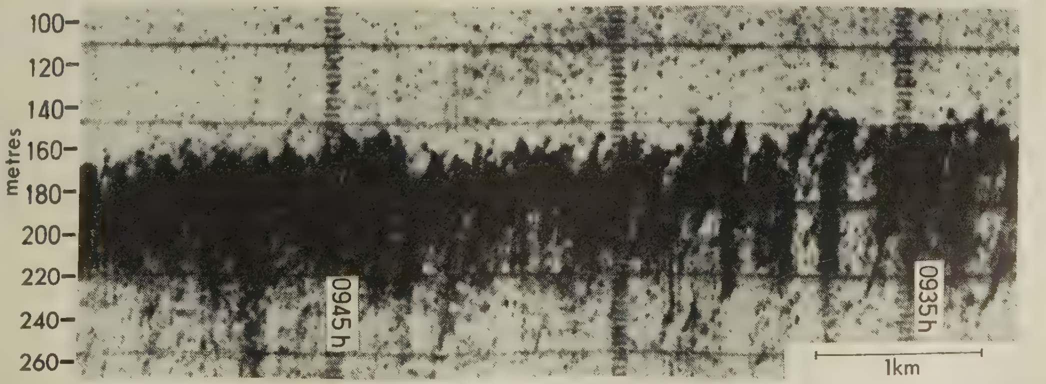
Moderate sized shoals recorded at 04·08–04·12 h at 9°20′W were present within 146 m of the surface. General tering was recorded down to 183 m. Ship speed 7 knots. Note sea floor echo on different phase.

At mid-day at approximately 11°05′W larger compact shoals are present at a minimum depth of 146 m. Most of general scattering was absent from the 55 to 200 m depth range. Ship speed 8·5 knots.

At 16·52 h at 12°30′W shoals appeared to be small and more sparse and seemed to be ascending to the surface. eral scattering was beginning to accumulate at a maximum depth of about 73 m. Ship speed 9·5 knots. Note sea r echo on different phase.

positions from which echo-traces reproduced in ures 3 to 28 were recorded. Echoes of the sea-floor not reproduced unless the phase on which they recorded happens to coincide with that of the tering shown. Where possible, environmental itions such as the approximate sea surface perature, sea state, wind force, etc., have been uded in the figure legends. Time given is Green- n Mean Time.

Due to inconsistency in the gain settings on some cruises and the effective range of the apparatus the more diffuse scattering layers which are known to be detectable at 10 kHz (Dickson, 1972) were not always recorded. Even so, many of the surveys carried out in daytime demonstrated the widespread occurrence of these layers in the deep ocean. The thickness of the layers varied considerably from 19 to 110 m. To the north of 50°N they were recorded to a maximum



ure 6. Vertical scale 95 m to 262 m. Trace obtained in mid-morning in April, 1971 at approximately 56°40′N 30′W. At a depth of 146–220 m numerous small discrete echoes probably due to blue whiting appear to merge form a layer trace. Ship speed 11·5 knots; gain maximum; sea floor 520 m; approximate sea surface temperature C; wind force 3; mean wave height 0·9 m.

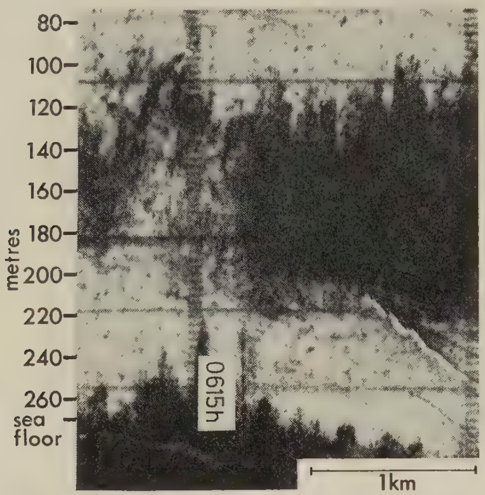


Figure 7. Vertical scale 74 m to sea floor. Trace recorded in early morning in April 1971 to the south of Rockall. One dense layer had just descended from the surface and is now seen to lie at depths between 110 and 220 m. In addition, scattering is seen near the sea floor and appears to merge with it. Ship speed 11·0 knots; gain maximum; approximate sea surface temperature 10·0°C; wind force 3; mean wave height 2·1 m; sunrise 04·40 h; moonrise 04·07 h; age moon 29 days.

depth of 330 m while farther south in deep oceanic water the maximum depth of the layers was sometimes in excess of 460 m. Diurnal migration between the surface and midwater was often apparent. Traces from single fish of high target strength near the surface was also widespread. Very much denser and larger discrete echoes were frequently recorded at various depths in daytime. Many are reproduced in this paper. In many cases repeated echo-surveys of the particular area from which they were obtained have produced similar types of trace. Gain settings given in the figure captions are relative. Most of the recordings obtained at night were not particularly informative. If dense traces were present they were often near the surface and had been obscured by the general scattering there, the whole often appearing as a continuous dense black layer.

Traces from daytime surveys conducted in summer between Latitudes 52°00′ and 60°00′N are shown in Figures 3 to 8. In this region discrete hyperbolic traces were abundant. The dense trace shown in Figure 3 was obtained early in the morning. Some general scattering had started to descend from the surface about half an hour previously, some still remains but now large discrete echoes from shoals are beginning to be discernable. Those shown in Figure 4 have a depth range of 146 to 293 m and are probably caused by a number of small fish shoals of relatively high target strength. Towards nightfa targets in this region often ascended to the surfac layers. As a result, the echoes sometimes tended t coalesce and a dense continuous layer was formed

It is well known that a dense shoal of fish may als disperse towards evening. This seems to be exempl fied in the traces shown in Figure 5 which wer recorded along an easterly–westerly transect at ap proximately 58°45′N in summer 1967, though c course one cannot preclude the possibility of spati variation in vertical distribution. In the early mornin (Fig. 5a) general scattering is present within th surface 183 m. Moderate sized shoals are seen to l at a depth range of 44 to 146 m. The mid-day trac taken further westwards is reproduced in Figure Large discrete shoals lie at depths in excess of 146 Towards evening and farther westwards (Fig. 5 very few large shoals are apparent. The hyperbol traces shown are almost certainly from small groups of fish which are probably gradually ascen ing to the surface.

Traces shown in Figures 6 and 7 were obtained spring to the south of Rockall. The few very sma echoes within the layer shown in Figure 6 are pr bably from single targets. These are intermingled wit larger echoes from shoals. The echoes are so num rous that they have coalesced forming a layer of

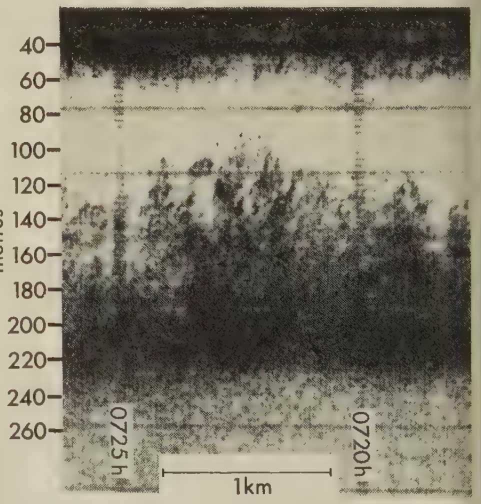
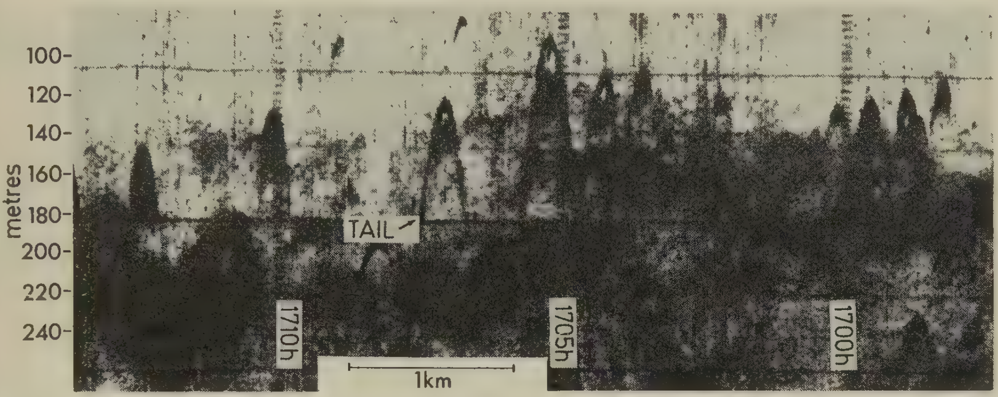
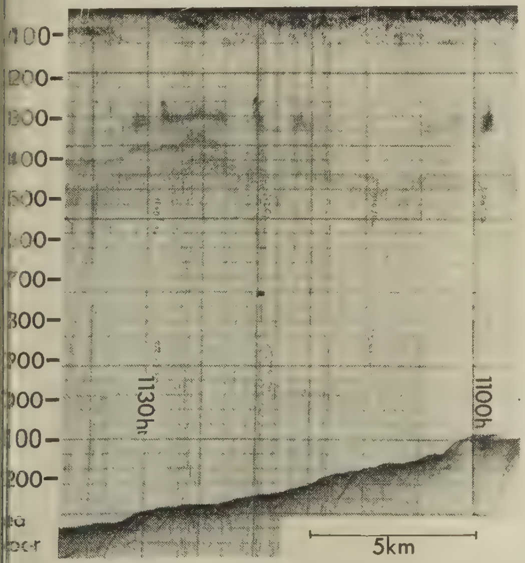


Figure 8. Vertical scale 18 to 290 m. Finely textur diffuse scattering most of which lies at a depth range 91 to 220 m was recorded at approximately 52°51 12°50′W in May 1971. This type of scattering is oft due to a relatively widely distributed mass of dispers fish such as myctophids. A few minute hyperbolae m be seen at the top of the layer. Ship speed 9·5 kno gain maximum; sea floor at 400 m; sea surface temp ature 11·6°C; wind force 6; mean wave height 2·6 sunrise 04·07 h.



re 9. Vertical scale 84 to 262 m. Classical comet-type echoes most of which are present between 90 and 212 m
e recorded at about 47° 55′N 8° 30′W in June 1967. These targets were extremely good reflectors of sound and are
ibly cetaceans. The white lines on some of the echoes are indicative of very dense aggregations. Most of the
ral scattering lies at a minimum depth of 146 m. Ship speed 11 knots; gain maximum; sea floor at 1883 m. Sea
ace temperature 13·6°C; wind force 4; wave height 0·6 m; sunset 19·55 h; moonset 21·36 h; age moon 00 days.

3 m thickness. Above and below this layer general
tering is sparse. This type of trace was often re-
ded during the spring and summer in oceanic wa-
o as far west as Longitude 20°W and as far south as Latitude 52°N. The trace shown in Figure 7 was recorded over shallower water and was probably from a similar target source as that in Figure 6. The echoes are very dense and numerous here and have coalesced completely; additional echoes may be



re 10. Vertical scale 18 to 1335 m. A recording
ined in mid-morning in April 1970 at approximately
0 N 18°47′W. General scattering lies within the
ace 110 m. The diffuse echoes here are probably
tc single fish. The small denser and rather irregular
hes are possibly due to loose aggregations of fish.
ll isolated shoals are between 247 and 329 m. Dif-
deep scattering layers are seen between 263 and
m. Ship speed 10·5 knots; gain maxium; sea floor
200 m; sea surface temperature 12·8°C; wind force
ean wave height 3 m.

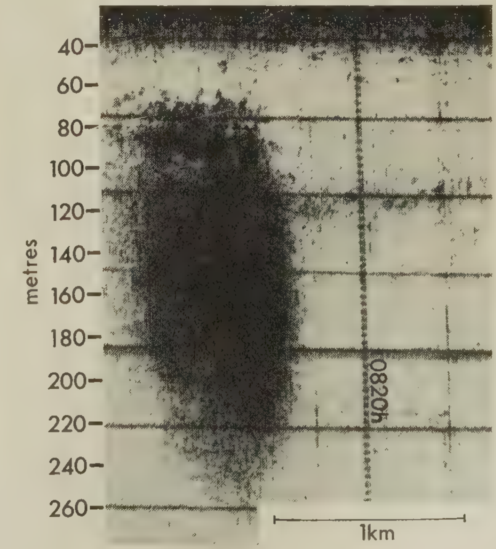


Figure 11. Vertical scale 18 to 272 m. Huge discrete spherical trace recorded in December 1969 at a position of about 43°00′N 13°00′W. Towards the top of the 'sphere' small hyperbolae from single targets may be distinguished. These gradually appear to merge as the depth increases partially as a function of the echo-display. Very little general scattering is present. Ship speed 10·5 knots; gain maximum; sea floor at 4846 m; sea surface temperature approximately 15·0°C; wind force 2; mean wave height 2·1 m; sunrise 07·21 h.

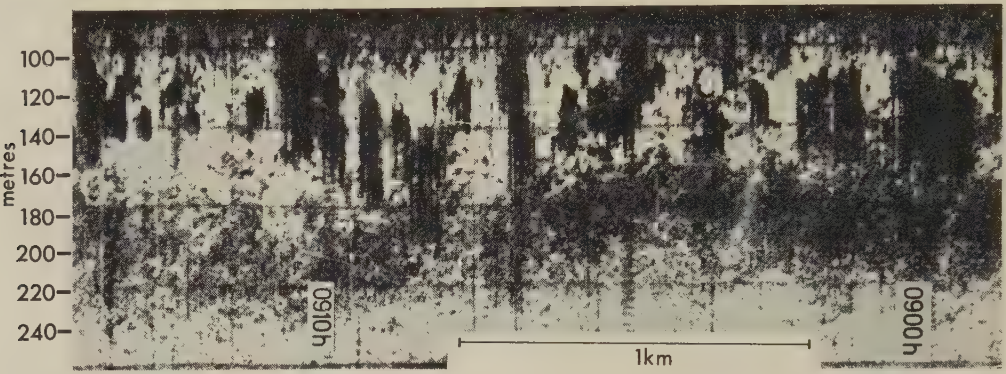


Figure 12. Vertical scale 75 to 265 m. Scattering of high density recorded within 220 m of the surface in April 1966 a 45° 50′N 7°40′W. Towards the top of the picture discrete echoes are visible, beneath these a denser layer trace m also be observed. The relatively low ship speed of 5·5 knots accentuates the horizontal extent of the echoes. Ga maximum; sea floor at 4689 m; sea surface temperature 13·0°C; wind force 6; mean wave height 4·2 m; sunri 05·08 h; moonrise 04·38 h; age moon 27 days.

seen near the sea floor. Most of the traces shown in Figure 3 to 7 are typical of those previously obtained from adult and larval blue whiting by Bailey (1971).

Very few diffuse layer-traces were encountered in the area to the north of 50°N. Notable exceptions occurred in relatively shallow water to the west of Ireland. An example is shown in Figure 8. Here a dense layer trace may be contrasted with the weaker diffuse but widespread deep scattering layers sometimes encountered in Atlantic oceanic water as shown in Figure 10. The fish forming this type of trace are likely to be of relatively low target strength and a dispersed. Small fish such as myctophids represe possible targets as they are known to be numerou in this region (Wheeler, 1969) and may produce layer trace (Schmidt, 1972).

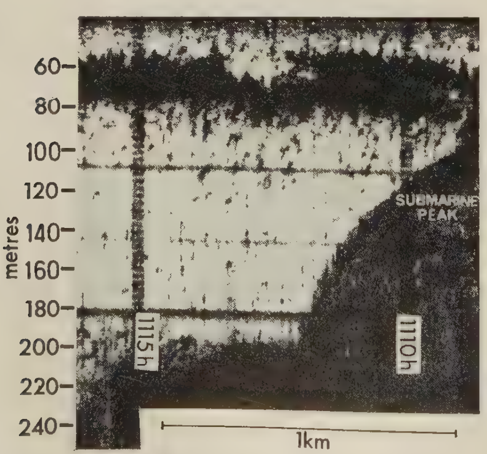


Figure 13. Vertical scale 37 to 255 m. A trace obtained at mid-day in May 1966 at approximately 43°05′N 20°30′W. The dense scattering layer lies at depths between 55 and 80 m and is probably caused by very small shoals and single targets packed closely together. The submarine peak is actually at 3000 m but is recorded on the same phase as the scattering. Ship speed approximately 6 knots; gain maximum; sea surface temperature 15·0°C; wind force 5; mean wave height 2·1 m.

Traces in Figures 9 to 23 were recorded betwee Latitudes 30° and 50°N. Here large variations i type of scattering were encountered and the trac sharply contrasted with those obtained farther nort wards. Traces from coastal or shallow water tende to be dense and complex whilst those recorded ov deep oceanic water were more sparse. The echoes Figure 9 were recorded off the southwesterly slop of the British Isles in early evening in summer. Pa

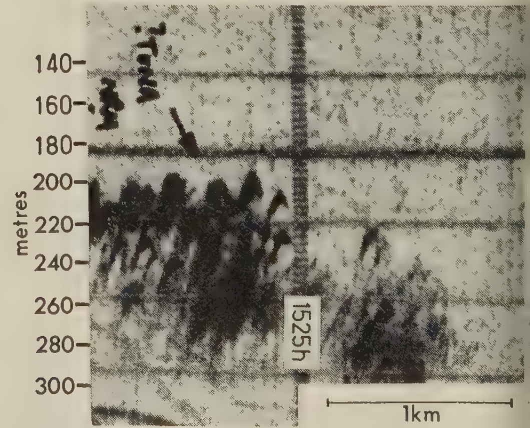
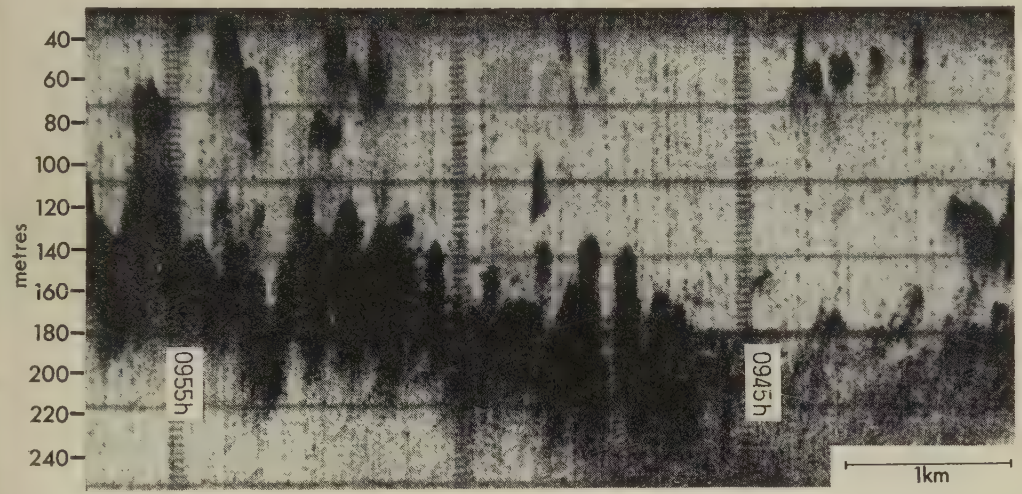
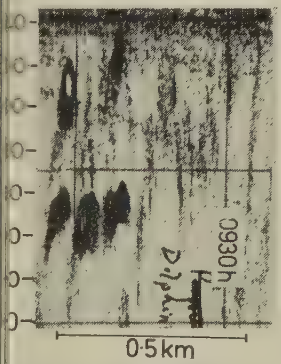


Figure 14. Vertical scale 112 to 316 m. Comet-trac possibly from tuna, recorded at depths between 192 a 296 m during an afternoon in September 1970 at ab 40°05′N 20°00′W. Ship speed approximately 10·5 kn gain maximum; sea floor at 4700 m; sea surface te perature 21·4°C; wind force 5; mean wave height 2·1



ure 15. Vertical scale 34 to 258 m. This was recorded in mid-morning in October 1970 just to the south of the
res. An extremely dense concentration of scattering may be seen in midwater. Most of this appears to be aggregated
roducing huge 'tower'-like traces. The scattering to the right of the picture at 183 to 256 m appears to be more
se. Ship speed 11 knots; gain maximum; sea floor at 2443 m; sea surface temperature 21·5°C; wind force 3;
e height 1·6 m; sunrise 06·00 h; moonset approximately 04·20 h; age moon 13 days.

of dense but diffuse scattering lie in midwater
epths below 146 m. Moderate numbers of very
e classical comets are also present. Those with
tails' are indicative of shoals nearest the centre of the sound cone. There is a considerable difference in range between the various shoals and the sounder. These shoals were particularly dense as shown by the white marks near the centre of some of the echoes. This is due to a 'white line' system described by various authors including Haines (1969) which operates when objects of very high target strength are recorded. This type of signal could be expected from cetacean shoals. Many other comet traces as well as layer traces were recorded in this region. However most 'comets' were slightly smaller and less well



re 16. Vertical scale 34 to
m. Discrete echoes probably
n dolphins recorded rela-
y near the surface in mid-
ning in August 1967 at ap-
imately 38°30′N 15°03′W.
'white lining' shown on two
es indicates the high target
gth of the shoals. The
ground marks are due to
noise. Ship speed 10 knots;
maximum; sea floor at
m; sea surface tempera-
approximately 5·0°C;
calm; sea calm; sunrise
0 h.

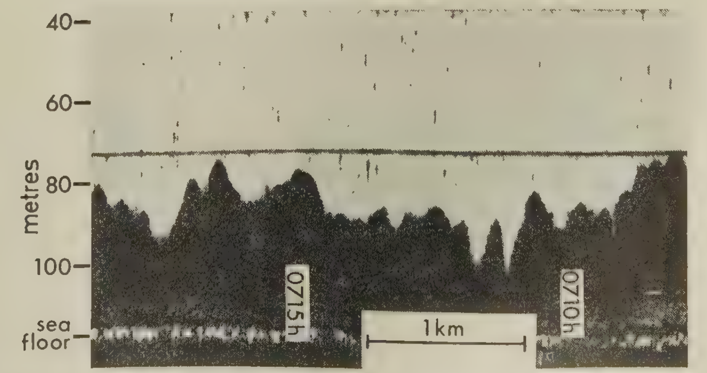


Figure 17. Vertical scale 37 m to sea floor. Dense layer trace recorded in early morning in September 1965. It lies in shallow water near the the sea floor at about 41°00′N 9°05′W and is similar to traces which have been shown to be due to pilchards. The marks above it may be caused by engine noise. Ship speed 11·5 knots; gain maximum; sea floor at 117 m; sea surface temperature 15·6°C; wind calm; sea calm; sunrise 0616 h; moonset 0757 h; age moon 18 days.

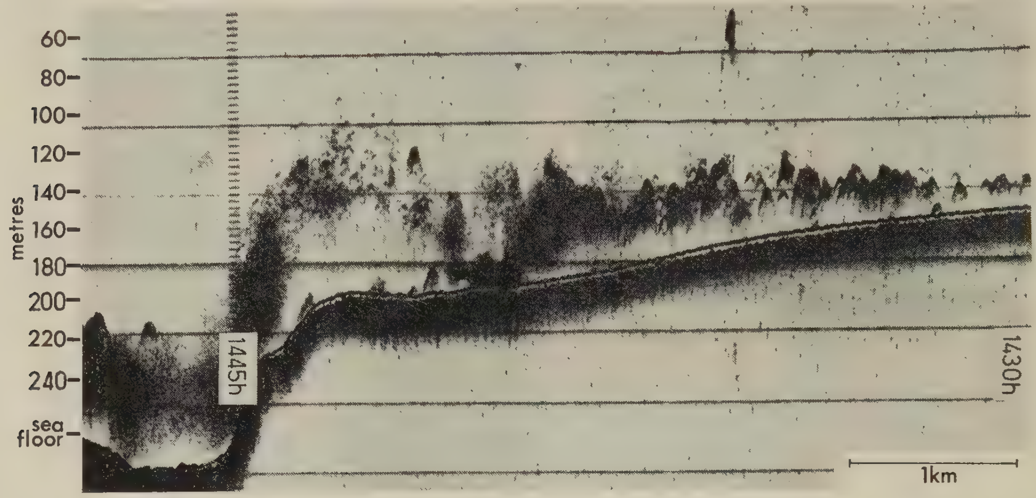


Figure 18. Vertical scale 50 m to sea floor. Complex trace recorded during an afternoon in September 1965 at approximately 39° 38′N 9° 30′W. To the left of the picture heavy diffuse scattering is seen to follow the contour of the sea floor and discrete echoes lie just above this. Traces from single targets are seen lying nearer the centre at a dept of 110 to 165 m. To the right numerous 'comets' may be seen just above the sea floor. Ship speed 10–11 knots; gain maximum – 6 dB; sea floor at 155–285 m; sea surface temperature 16·5°C; wind force 3; sea calm.

defined than those shown and were more likely to have been caused by shoaling fish.

Figure 10 demonstrates the presence of the small amounts of scattering sometimes recorded over deep oceanic water. Small compact isolated fish shoals are shown in midwater. General scattering lies within the surface 110 m and also between 263 and 460 m. The recording shown in Figure 11 demonstrates a discrete shoal of a considerable size. Only two such shoals were encountered during the survey in this particular area. They were spaced approximately 7 km apart. All other types of scattering were sparse.

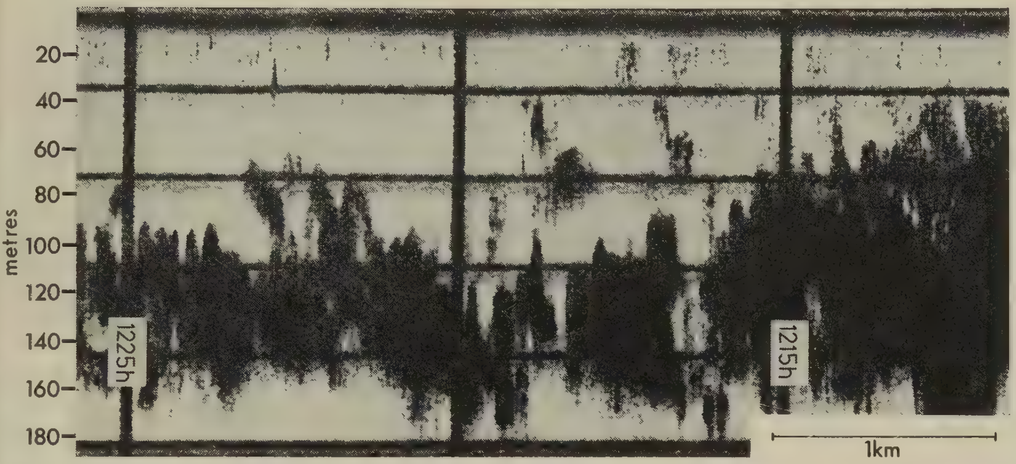
During the surveys over deep water in Biscay in spring 1966 targets were repeatedly recorded. A typical picture is shown in Figure 12. Numerous dense discrete echoes probably from fish shoals are present within the surface 200 m. Many of the discrete echoes recorded in this area were elongated and irregular in form. Sometimes they were so numerous that they seemed to coalesce, a situation accentuated by the presence of moderate quantities of general scattering.

Other areas of interest included water in the vicinity of steep submarine elevations. Although the mountainous sea floor was often a considerable way below the sea surface, recordings over them frequently demonstrated the presence of dense scattering in midwater. Figure 13 demonstrates scattering obtained in daytime in spring at an approximate position of 43°05′N 20°30′W. The peak on the right of the picture is recorded on a different phase and lies at approximately 3000 m. A dense scattering layer is present between 55 and 80 m. The genera scattering below 180 m is moderate in extent.

The trace in Figure 14 was recorded over dee water in summer at approximately 40° 05′N 20° 00′W The asymmetry of the hyperbolae is due to tilting o the transducer. Here are shown some of the isolate groups of dense discrete shoals which were intermittently recorded in this region. These traces ar typical of those previously obtained from tuna b Shibata and Nishimura (1969). Figure 15 show some of the densest scattering recorded in daytim during the "Discovery" surveys in the North-easter Atlantic. It was obtained close to the Azores in 197 and clearly demonstrates the dense concentration o targets often found near oceanic isles. In the record are seen some huge tower-like vertically elongate shoals which appear to be very closely aggregated

Also of interest but not typical of the sparse are in which they were recorded are the dense, wel defined comet traces shown in Figure 16. These wer probably produced by dolphins which had followe the ship for most of the day during a cruise in summer 1967.

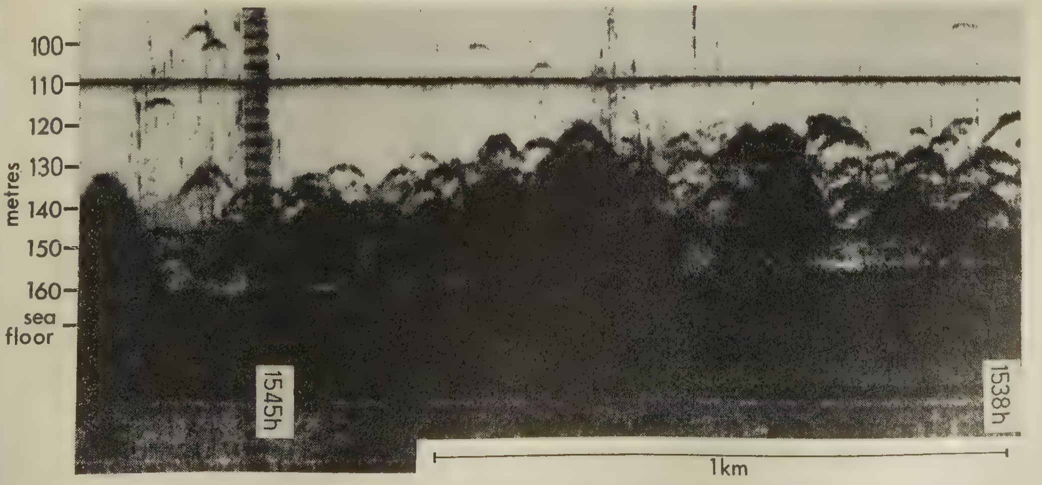
Greater diversity was apparent in European an African coastal water. The mountainous trace show in Figure 17 was recorded off the Portuguese coa in summer 1965 and is similar to that shown b Cushing (1963) to be due to pilchards. In contra the traces in Figure 18 obtained in coastal water little farther to the south appears to be of great



ire 19. Vertical scale 5 m to 186 m. This dense trace recorded at mid-day in March 1960 near 36°10′N 6°20′W ns to consist of a number of vertically elongated echoes which have coalesced. Traces somewhat similar to this known to be caused by anchovy shoals. Ship speed 9·5 knots; sea floor at approximately 915 m; sea surface perature 15·0°C; wind force 6; mean wave height 1·2 m.

plexity. Diffuse scattering as well as hyperbolic oes from shoals and single targets is in evidence. ; suggests the possibility that a variety of fish i different shoaling characteristics are present in area. The extremely dense vertically elongated of trace shown in Figure 19 was recorded near outlet of the Mediterranean Sea in spring 1960. nicki (1970) has previously shown that anchovy produce a similar type of picture. Few record- were made near the Moroccan Coast. However one shown in Figure 20 which was recorded in autumn 1966 was particularly well defined. Here a considerable number of fish appear to be present.

Recordings over the steep slopes near the Island of Madeira in daytime invariably produced large dense but discontinuous traces. Small 'spot' and 'fingernail' traces were also sometimes recorded. The trace in Figure 21 was obtained in summer 1965. Huge compact comets are produced by shoals which lie within 146 m of the surface just off the Island slope where one could expect to find nutrient-rich water. These targets are of very



ire 20. Vertical scale 80 m to sea floor. During the recording the ship was travelling at about 6 knots. The small rete echoes of constant minimum vertical thickness ('fingernail' traces) are indicative of single targets. These are tered amid moderate-sized shoals. Most targets are near the sea floor. Recorded in November 1966 at approxiely 33°55′N 7°50′W; sea surface temperature 18·8°C; wind force 2; sea calm; sunset 16·57 h.

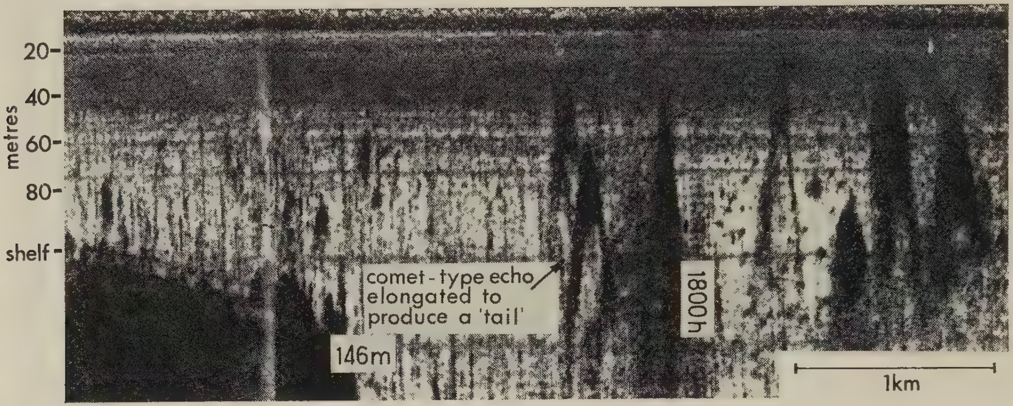


Figure 21. Vertical scale surface to 168 m. Large comet-traces recorded towards evening in September 1965 to the north of the Island of Madeira. Targets are abundant near the steep slopes of the island shelf. Ship speed 11·5 knots; gain estimated at maximum −6 dB; sea surface temperature 22·9°C; wind force 5; mean wave height 1·5 m; sunset 19·06 h; moonset approximately 18·00 h; age moon 25 days.

high signal strength as indicated by the density of the apical part of the comet and the very long 'tails'. Smaller shoals are present farther inshore.

The effect of diurnal behaviour upon the type of echo trace obtained in deep oceanic water which was frequently observed between Latitudes 24°N and 36°N is demonstrated in Figure 22. Here a weak diffuse deep scattering layer is seen in midwater. A second layer is seen migrating towards the surface, appearing to become denser as it does so. In addition discrete shoals are migrating to the surface. During the hours prior to this very few echoes were recorded. Rarely were shoals recorded during the morning descent. A notable exception was apparent at approximately 30°N 22°00′–22°30′W in March 1972, when numerous dense comet traces were obtained near the surface during the night. Before dawn some shoals appeared to descend to midwater as shown in Figure 23. None were detected after 05·50 h when presumably they exceeded the range of the sounder.

The trace shown in Figure 24 has been included because it shows the effect of ship speed on the type of trace produced. It was obtained near the Canary Isles in early evening in December 1969. General scattering in this region is fairly dense. Amid this, dense comet traces lie at a depth range of 37 to 119 m.

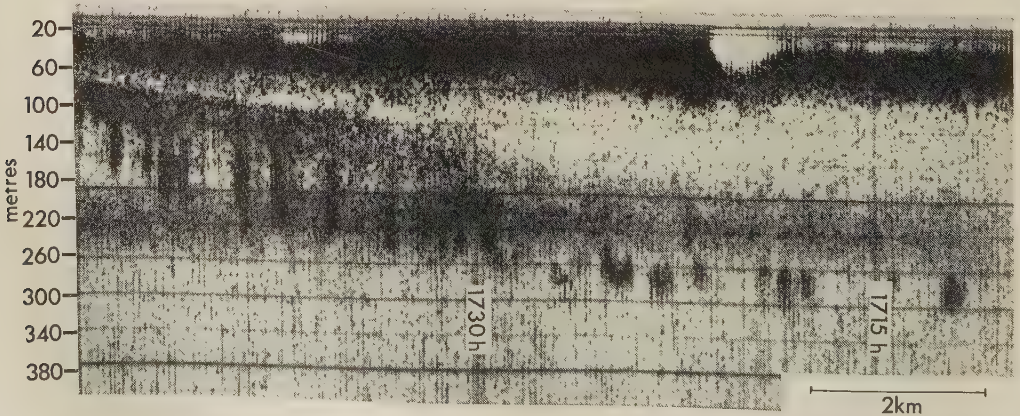


Figure 22. Vertical scale surface to 398 m. Shoals are seen migrating from 300 m towards the surface at 17·10–17·47 h. Initially they appear in mid-water as discrete 'comets' but as they ascend the echoes become vertically elongated. One diffuse layer is seen at a depth range of 183–256 m. To the left of the picture another diffuse layer is seen in the process of vertical migration. Recorded in March 1962 at approximately 30°05′N 24°02′W. Ship speed 9·5 knots; gain maximum −6 dB; sea floor at 2840 m; sunset 17·45 h; wind force 6; mean wave height 3·3 m; moonset approximately 12·45 h; age moon 25 days.

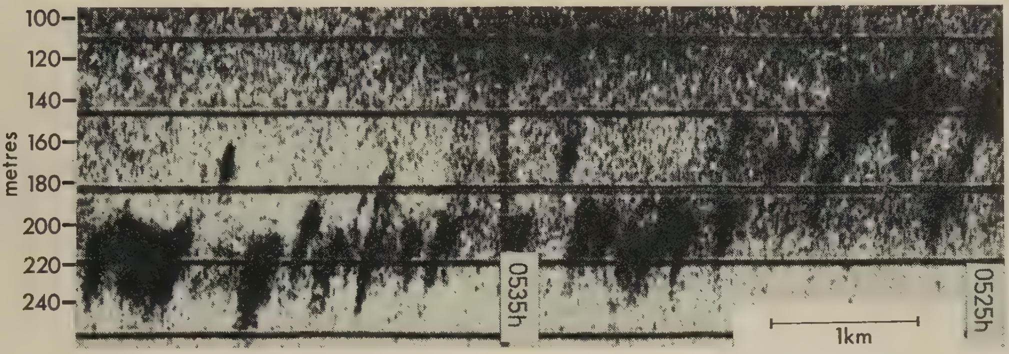


Figure 23. Vertical scale 96 to 263 m. A type of trace infrequently recorded at dawn in the oceanic water of the Northeastern Atlantic. This was obtained in March 1972 at approximately 30°00′N, 22°00′–22°30′W. A large number of discrete shoals are seen at 05·25 h at the start of a morning descent. In addition general scattering is present within 230 m of the surface. Ship speed 11 knots; sea floor at 4950 m; sea surface temperature 18·5°C; wind force 4; mean wave height 0·9 m; sunrise 06·34 h; moonset 06·05 h.

When the ship is stationary single targets are easily resolvable and the general scattering erroneously appears to be less dense than that recorded at high speed.

Recordings obtained in North-west African coastal water in 1968 demonstrate the diversity in type of scattering there. The increased diversity contrasts with that recorded in the sparser deep oceanic water (Fig. 10). In Figure 25 are seen vertically elongated shoals many of which appear to be demersal. This type of echo is similar to that previously recorded from sardines (Furnestin, 1953). The trace in Figure 26 contrasts in that the majority of scattering appears as a continuous dense layer which becomes more diffuse with increasing depth. The dense deep undulating layer shown in Figure 27 was recorded continuously over slopes in the same region and may have reflected water movements due to internal waves.

The 'comets' shown in Figure 28 were recorded near the Cape Verde Isles in 1969. These are also similar to traces shown by Shibata and Nishimura (1969) to be derived from tuna. Hardly any other type of scattering was recorded here except some rather diffuse traces near the surface probably caused by single fish.

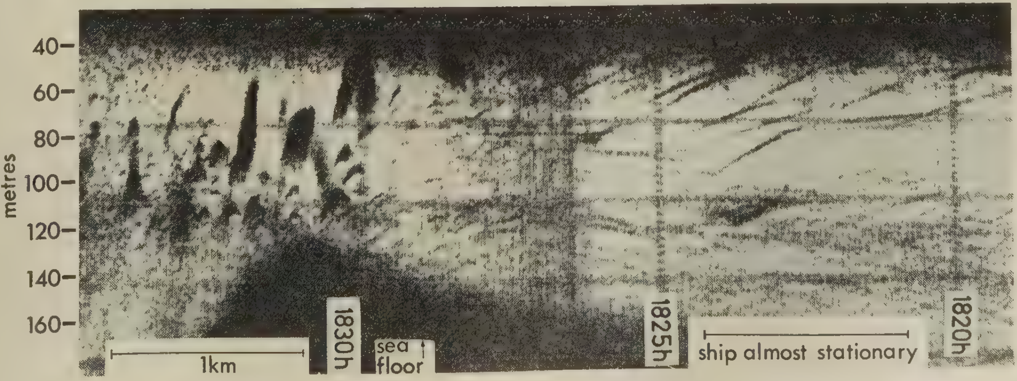


Figure 24. Vertical scale 28 m to 190 m. Recording to show how a trace may be affected by ship speed. To the right of the picture the ship is almost stationary and individuals which here appear to be diving are recorded as discrete oblique streaks of constant minimum vertical thickness. Towards the centre of the picture these traces of single targets have become reduced in horizontal extent due to an increase in ship speed. Fewer individuals are now resolved. The traces to the left of the picture were recorded at a ship speed of 10 knots. Now compact discrete echoes which indicate shoaling are seen and many of the single targets merge together and form some of the general scattering. Recorded to the east of the Canary Isles in early evening in December 1969. Gain maximum; sea floor at a minimum of 136 m; sea surface temperature 21·5°C; wind force 7; mean wave height 1·5 m; sunset 17·13 h.

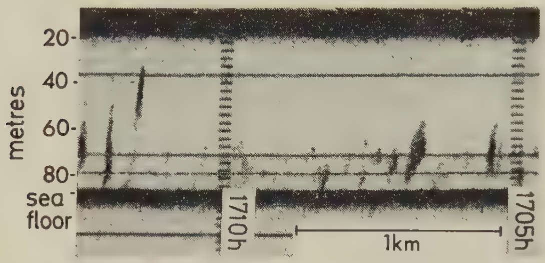


Figure 25. Vertical scale surface to 90 m. Vertically elongated fish traces similar to those from sardines were recorded between 36 m and the sea floor at 22°00′N 17°25′W in early evening in January 1968. Ship speed approximately 9 knots; sea surface temperature 17·0°C; wind force 6; wave height 1·2 m; sunset 18·04 h.

Discussion and conclusions

Types of trace recorded during the "Discovery" cruises in the North-eastern Atlantic varied to a great extent. Most echoes were typical of those known to be produced by fish. In addition some very large dense discrete echoes were likely to have been due to the presence of cetaceans.

The echo traces were undoubtedly very variable towards the shallow coastal water. This seems likely to reflect the different shoaling characteristics exhibited by various types of target. However one cannot be certain of this for it is known that some species of fish produce various types of trace depending on whether they happen to form reproductive or feeding shoals (Cushing, 1973).

Generally it should be possible to gain a comparative estimate of shoal size from the horizontal and vertical extent of a trace but it is important to take

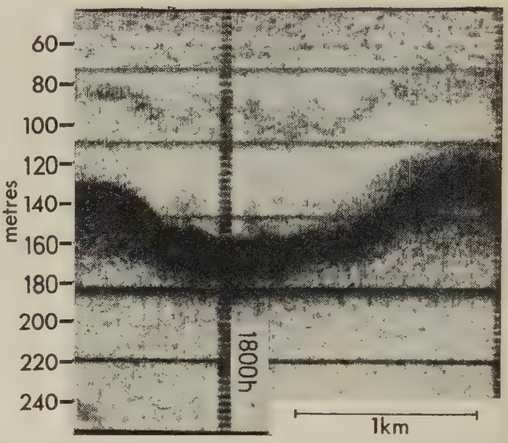


Figure 27. Vertical scale 36 to 250 m. Trace obtained during early evening in February 1968 at 18°50′N 16°50′W. A continuous layer lies at a depth range of 110–179 m. The undulations may possibly be correlated with the presence of internal waves. Ship speed approximately 10 knots; sea surface temperature 17·9°C; wind force 4; mean wave height 0·9 m; sunset 17·43 h; moonset approximately 01·03 h.

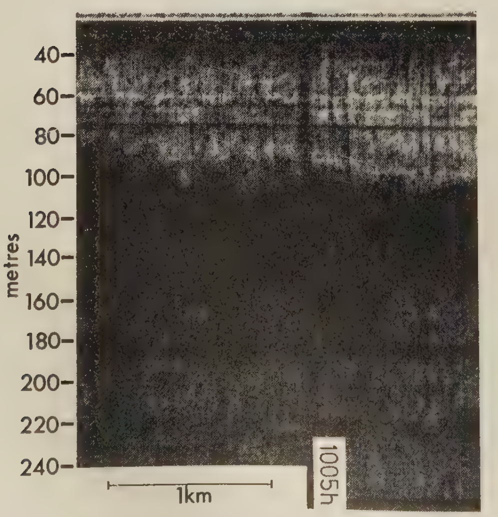


Figure 26. Vertical scale surface to 260 m. Dense layer trace recorded in mid-morning in February 1968 at 19°25′N 17°15′W. Sea floor at a minimum depth of 1150 m. Ship speed 11 knots; sea surface temperature 16·0°C; wind force 6; mean wave height 1·2 m; sunrise 06·49 h.

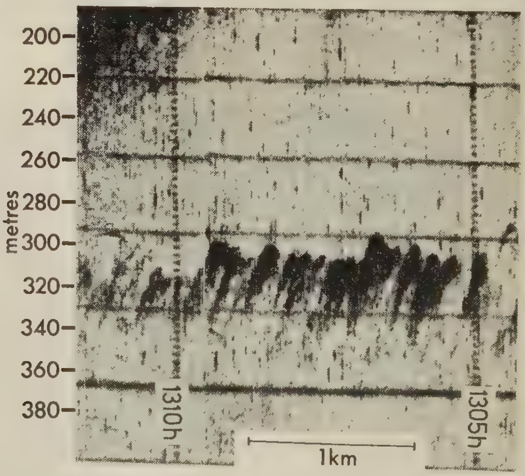


Figure 28. Vertical scale 183 to 402 m. The discrete comets which are present at 293 to 329 m are very similar to those sometimes recorded from tuna. This trace was obtained in November 1969 near the Cape Verde Isles. The steep submarine elevation has a minimum depth of 1500 m. Ship speed 11 knots; gain maximum; sea surface temperature 26·9°C; wind force 5; sea calm.

into account the fact that sampling with the NIO precision echo sounder at any one time occurs in a single plane. A further factor is that discrete shoals near the periphery of the beam may appear to be reduced slightly in vertical extent. However, the survey covered a considerable area, and targets were sampled at random and so a representative cross-section of scattering was thought to be obtained.

The extent and density of the discrete echoes and layer traces particularly from some of the shallower areas of the Atlantic demonstrates a considerable abundance of single and multiple biological targets. The more widespread and weaker deep scattering layers suggest the presence of more sparsely distributed single targets. It is very difficult to estimate abundance of the latter for it has been shown that single targets as far as 10 m apart may produce a layer trace.

Despite the limitations it is thought that a comparative study of the traces reproduced may prove to be of interest to biologists and also to geologists who often find that biological sound scattering may interfere with sonar displays of the sea floor.

Acknowledgements

I would like to thank colleagues who participated in the collection of data and also the staff of the Institute of Oceanographic Sciences who prepared the figures. I am also indebted to Dr D. H. Cushing and Mr A. R. Stubbs who advised on the interpretation of the traces and to Mr P. M. David who advised on the manuscript.

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On changes in some biological parameters in the North Sea sole (*Solea solea* L.)

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Biological parameters such as length and weight-at-age, fecundity and length at first maturation, derived from market sampling in Dutch ports, showed significant changes in the period under observation 1957–1973. An attempt was made to correlate these changes with environmental factors such as the density of the sole stock, temperature in the growth-season, eutrophication, and fishing effort. Of these factors significant correlations were only found with fishing effort and with indices of the disturbance of bottom layers by active gears. Additional evidence points to the possibility that the amount of beam-trawling with chains has a positive effect on the growth rate and on other biological parameters of the sole.

Introduction

The sole fishery in the North Sea is a matter of great concern both to fishermen and to administrators. A fast expansion in the sole fishing fleet in the Netherlands since 1966 has led to a situation of increasing overfishing. The ICES North Sea Flatfish Working Group has reported repeatedly on the situation (ICES, 1970; 1973a and 1973b; 1974; 1975) and has given advice on measures to improve the situation in the fishery.

The sole stock has declined markedly since 1967–1968, when the very strong 1963 year class, responsible for the high stock level in 1966, started to lose its importance and recruitment fell to a lower level. The unfavourable situation in the sole fisheries has ultimately led to restrictions of fishing by means of catch quota imposed by the North East Atlantic Fisheries Commission from the 1 January 1975 onwards. The aim is to bring the fisheries back to more favourable conditions and give the sole stock an opportunity to recover by setting appropriate Total Allowable Catches annually.

Overfishing in the North Sea sole stock is only a relatively recent feature. In general terms the stock has been under-exploited in the period before 1963–1964 and moved quickly through a period of optimum fishing effort in 1965–1966 to ever increasing overfishing in the years after 1966.

For the Netherlands the sole has become the major fish species and an extensive sampling programme has made it possible to follow the developments in the sole stock closely. Dutch fishermen catch soles all over the southern and central North Sea and the sampling has been spaced in time and place to cover all parts of the exploitation area. Since 1957 sole landings at IJmuiden, and in later years in other ports, have been sampled weekly on a routine basis in order to follow the length and age compositions of the various sole substocks exploited by the Dutch fishermen. Data on the maturation of female soles have been collected from 1962 onwards including the weight of the ovaries as an index of fecundity. Prior to market sampling length-at-age data were available for the second quarter of the year from research ship sampling along lines of stations perpendicular to the Dutch coast from 1951–1956 (Boerema, unpublished). In the years concerned the available data showed changes in growth, maturation and fecundity which will be discussed here.

Variations in length-at-age

Generally Dutch fishermen tend to concentrate on small to medium-sized soles although a number of them go to fishing grounds where the large soles are taken. Growth data from the landings may be biased by the dominance of the smaller soles. During the spawning season soles of all lengths and ages aggregate in the shallow coastal waters for spawning and length-age data from this period supposedly

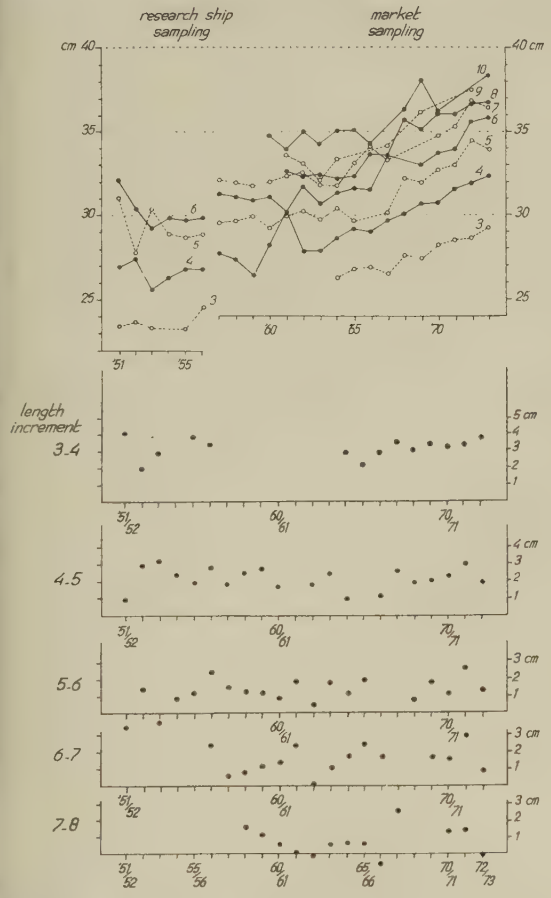

Figure 1. Top diagram, average length-at-age for North Sea sole, sexes combined, in the second quarter, based on research ship sampling 1951–65 and commercial ship sampling in the fish market 1957–73; other diagrams, annual length increments by years.

provide a more adequate picture of the real growth in the sole stock. Therefore, the second quarter – the months of April, May, and June – was selected as a basis for calculating average length-at-age for males and females. Table 1 gives these values together with the standard error and the total number of otoliths in the length-age keys used in the conversion of length into age distributions. Figure 1 shows the average lengths for sexes combined in the upper diagram together with the values derived from research ship sampling at fixed stations in 1951–1956. To make research vessel data and market data comparable a correction for shrinkage has been applied (ICES, 1965, Fig. 20) of 1·5 mm for soles of 20 cm, 3·5 mm for 25 cm, 4·5 mm for 30 cm and 5 mm for 35 cm.

It is obvious from the upper diagram of Figure 1 that the average length-at-age for the soles sampled in the fish market is not constant but shows a steady increase from about 1963 onwards. The influence of the individual year classes cannot be traced easily. In order to study the growth curves for each year class Figure 2 shows the length-at-age in the second quarter by year class. It is apparent that the growth curves of the individual year classes do differ and that the more recent year classes have increasingly steeper growth curves.

The average lengths from the sampling on fixed stations in the period 1951–1956 appear to be at a somewhat lower level than the corresponding values in the market sampling from 1957–1962. It is possible that a change in growth had started before 1962. On the other hand the research ship data cover only a small part of the total exploitation area and the observed differences may reflect differences in growth in different sole sub-stocks. From 1968 onwards the sampling has been intensified in order to cover all different sole sub-stocks more adequately as shown in Figure 3. The average length-at-age for the sub-stocks in the second quarter of the years 1968–1973 is given in Table 2 for males and females. For the age-groups 4, 5 and 6 the length values for sexes combined are shown in Figure 4 for the most important sub-stocks.

Apparently all four sole sub-stocks demonstrated an increase in growth and no significant difference in length-at-age values exists between the sub-stocks in the period 1968–1973. This implies that the factors responsible for the observed increase in growth are not restricted to certain areas. Their influence extends all over the part of the North Sea under consideration. Although insufficient data are available for the pre-1968 years, it seems reasonable to assume that the growth of the various sole sub-stocks were identical not only for 1968–1973 but also for the preceding years. Thus in our search for the factors responsible for the increase in growth the length-at-age data for all sub-stocks combined as given in Table 1 and Figures 1 and 2 may be used as representative for all sub-stocks.

When investigating the annual increments of length (Fig. 1, lower diagrams) it is obvious that for the age-groups 3 and older no significant increases in increments took place from 1951 onwards. Consequently the increase in growth must have taken place in the youngest age-groups. Unfortunately long term data on the lengths of soles younger than 3 years are lacking. However, length data of 0-group soles can be derived by the Petersen method from the data given by Meyer-Waarden and Tiews (1965) and Tiews (1971) for the German nurseries for the period 1954–1967 and data from the Netherlands–

Table 1. Average length ($\bar{l}$), standard error ($S\bar{l}$), and number of otoliths use

Year	Age-group	3*		4		5		6		7		8	
		$\bar{l}$	$S\bar{l}$	$\bar{l}$	$S\bar{l}$	$\bar{l}$	$S\bar{l}$	$\bar{l}$	$S\bar{l}$	$\bar{l}$	$S\bar{l}$	$\bar{l}$	
1957	♂	25·0	0·4	25·9	0·4	28·8	0·7	29·8	0·6	29·4	0·4	31·1	0
	♀	26·0	0·2	28·6	0·3	31·0	0·8	33·1	0·6	34·8	0·4	37·4	0
1958	♂	26·0	0·4	27·4	0·6	27·5	0·4	28·2	0·6	29·4	1·0	30·7	0
	♀	26·9	0·6	29·5	0·3	31·9	0·3	32·4	0·6	35·1	0·8	33·6	0
1959	♂	25·5	0·4	25·7	0·3	27·5	0·4	28·7	0·6	28·4	–	31·2	0
	♀	26·5	0·2	29·0	0·4	32·2	0·4	33·0	0·7	35·2	1·6	36·1	0
1960	♂	26·7	0·4	26·4	0·3	26·8	0·5	28·1	0·4	28·9	0·5	29·4	1
	♀	26·9	0·4	29·9	0·3	31·6	0·6	34·0	0·3	35·1	0·4	–	
1961	♂	25·8	0·2	28·9	0·3	27·9	0·6	27·9	0·9	30·5	0·5	29·4	0
	♀	26·5	0·2	31·6	0·5	32·0	0·5	32·3	0·5	34·2	0·7	35·7	0
1962	♂	26·2	0·6	26·4	0·1	27·8	0·5	29·1	0·5	29·5	0·7	29·6	0
	♀	26·0	0·2	29·2	0·2	32·6	0·5	34·4	0·3	35·4	0·4	35·2	0
1963	♂	25·4	0·4	27·1	0·5	27·7	0·2	28·1	0·4	29·4	0·4	29·3	0
	♀	26·2	0·2	28·6	0·5	31·7	0·2	33·2	0·4	34·2	0·5	35·4	0
1964	♂	26·5	0·3	26·9	0·2	28·0	0·3	29·2	0·2	29·4	1·4	30·1	0
	♀	26·1	0·2	30·3	0·4	32·7	0·4	33·5	0·1	33·9	0·3	34·3	0
1965	♂	25·4	0·5	28·7	0·5	27·8	0·2	29·7	0·7	31·0	0·3	29·2	0
	♀	28·2	0·8	29·6	0·5	31·4	0·6	33·5	0·6	35·1	0·3	35·4	0
1966	♂	26·3	0·2	–	–	–	–	27·8	0·7	31·8	0·5	31·3	0
	♀	27·4	0·1	29·4	0·4	35·0	1·4	35·2	0·4	36·4	1·0	36·0	0
1967	♂	25·7	0·2	28·3	0·1	29·6	0·3	30·2	1·1	30·3	0·5	29·4	0
	♀	27·2	0·2	31·0	0·1	30·6	0·4	36·8	1·1	36·3	0·4	37·5	0
1968	♂	26·2	0·2	27·9	0·2	30·2	0·2	–	–	–	–	33·1	0
	♀	29·0	0·4	32·1	0·2	34·1	0·1	32·7	1·2	40·3	0·5	38·2	0
1969	♂	26·3	0·1	28·6	0·2	29·8	0·2	30·9	0·1	–	–	31·5	1
	♀	28·4	0·1	32·5	0·3	33·9	0·2	35·1	0·1	38·4	0·7	38·6	0
1970	♂	27·3	0·1	29·0	0·2	30·7	0·4	31·5	0·2	32·2	0·1	–	
	♀	29·1	0·1	32·3	0·1	34·7	0·3	35·8	0·3	37·1	0·1	37·7	1
1971	♂	27·9	0·1	30·1	0·1	31·4	0·2	31·2	0·4	33·2	0·3	33·6	0
	♀	29·0	0·1	32·8	0·1	34·5	0·2	36·6	0·3	37·3	0·3	38·4	0
1972	♂	27·8	0·1	30·6	0·2	32·4	0·2	33·6	0·5	34·6	1·5	34·1	0
	♀	29·4	0·1	33·1	0·2	36·6	0·2	37·5	0·3	39·0	0·4	39·3	0
1973	♂	28·2	0·1	30·4	0·1	31·6	0·4	33·3	0·4	33·0	0·5	33·1	0
	♀	30·5	0·2	34·2	0·1	36·2	0·4	38·2	0·3	39·8	0·5	40·2	0

* This age-group only partly recruited in the period 1957–1967 and average length can thus be assumed to be biase
these years.

Belgian–German Waddensea programme for 1969 onwards. Additional data on 0-group length is given by De Clerck (1974) for the Belgian coast and for the pre-war situation by Tesch (1913) and Bückmann (1934) for the Dutch and German nurseries respectively.

Figure 5 shows the modal length of 0-group soles in the German coastal area in 1954–1967 and in the Dutch Waddensea and the Belgian coast in 1969–1972. Tesch (1913) and Bückmann (1934) give about 9 cm as the average length after one year. It may be concluded that no significant change took place in the average length until about 1964. After that time a small increase can be observed to 10 cm at present. This increase is only 1 to 1½ cm over the last ten years whereas, for example the 4 year old soles changed from 28 cm to 32½ cm, an increase of 4½ cr in the same period. Therefore, the main increase ir length-at-age should have taken place in the seconc and the third year of life. Soles of that age are no distributed all over the North Sea. After having lef the nurseries their distribution is limited. The factor responsible for the increase in growth in the sol have to be localised in the coastal waters of th North Sea but outside the estuaries and the Waddensea.

Variations in weight-at-age

Table 3 gives the gutted weight-at-age with gonad for males and females in the second quarter. Fo gth-age key for North Sea sole in the second quarter, derived from market-sampling

9		10		11		12		13		14		15		Total number of otoliths (n) in length-age keys (including age-groups 15+)
$\bar{l}$	$S_{\bar{l}}$	$\bar{l}$	$S_{\bar{l}}$	$\bar{l}$	$S_{\bar{l}}$	$\bar{l}$	$S_{\bar{l}}$	$\bar{l}$	$S_{\bar{l}}$	$\bar{l}$	$S_{\bar{l}}$	$\bar{l}$	$S_{\bar{l}}$	
32·3	0·4	32·1	0·6	–	–	–	–	–	–	–	–	–	–	94
37·6	0·7	38·0	0·5	–	–	42·0	2·0	43·1	2·0	–	–	37·0	2·2	203
32·1	1·3	31·0	1·4	31·7	0·6	–	–	–	–	–	–	–	–	127
34·7	1·3	37·6	0·7	38·4	0·5	–	–	–	–	–	–	–	–	176
30·5	0·2	29·5	2·2	–	–	31·8	1·3	–	–	–	–	–	–	49
34·3	0·5	38·2	1·1	38·3	1·4	39·1	0·8	37·5	0·3	–	–	–	–	142
–	–	30·8	0·7	–	–	–	–	32·7	0·7	–	–	–	–	114
40·1	0·6	38·7	0·5	37·8	0·9	37·7	0·9	40·6	0·7	–	–	–	–	183
32·7	0·7	31·2	0·8	31·8	0·5	34·5	0·7	34·4	1·4	35·5	0·8	–	–	97
34·4	1·3	36·5	0·9	37·8	0·9	39·0	1·0	31·8	1·7	39·9	0·7	–	–	252
28·3	0·7	–	–	31·2	1·0	30·5	0·7	33·1	1·0	34·7	1·3	35·4	0·9	184
37·8	0·4	38·5	1·5	37·7	0·7	41·5	0·8	40·0	0·7	41·5	0·5	40·8	0·4	318
30·7	0·7	30·3	1·0	32·7	1·2	33·3	0·8	34·1	1·1	34·1	1·6	34·4	1·6	252
33·4	1·4	38·0	0·6	38·9	0·6	–	–	40·8	0·9	38·8	0·3	40·5	1·6	354
30·9	0·4	32·4	1·2	32·4	0·8	33·5	2·3	36·8	0·6	31·7	0·8	33·8	1·4	344
35·8	0·5	37·8	0·4	36·2	0·9	38·7	0·8	38·5	0·5	39·0	0·7	42·3	0·4	504
–	–	31·6	1·2	–	–	31·6	1·4	33·9	0·4	34·5	1·0	–	–	120
40·3	0·8	38·6	0·7	37·1	0·6	42·0	0·8	37·3	1·8	–	–	41·7	1·5	146
–	–	31·7	0·4	–	–	–	–	32·0	0·8	–	–	–	–	147
6·5	0·6	36·7	0·7	41·1	1·2	38·2	0·8	42·2	0·8	–	–	42·8	0·3	381
1·2	0·3	–	–	31·1	1·2	30·2	1·9	32·7	1·3	33·2	1·1	–	–	423
6·9	0·3	36·9	0·6	38·7	0·5	38·4	1·3	39·4	0·4	41·0	0·5	41·2	1·7	773
–	–	33·0	0·4	–	–	34·2	0·6	–	–	–	–	–	–	400
8·0	1·1	39·5	0·4	42·9	1·1	42·0	0·5	39·2	1·5	41·0	0·6	–	–	502
3·3	0·5	–	–	34·2	0·5	–	–	33·5	0·9	33·5	1·2	34·8	1·2	934
9·1	0·3	39·6	0·4	40·2	0·3	39·7	1·2	42·3	0·4	44·2	0·8	44·2	0·7	1 248
–	–	33·3	0·4	35·3	0·4	34·1	0·1	35·7	0·9	32·4	0·1	34·6	1·0	1 301
–	–	39·0	0·2	38·6	0·7	40·1	0·2	43·0	0·7	41·2	0·5	42·0	0·6	1 736
–	–	–	–	35·0	0·1	–	–	36·3	0·4	–	–	–	–	936
–	–	–	–	39·5	0·2	–	–	40·5	0·4	39·7	1·9	40·4	1·0	1 170
4·6	0·2	–	–	–	–	33·7	0·7	–	–	36·6	0·4	–	–	978
0·3	0·2	40·8	1·9	40·8	3·9	41·5	0·9	40·3	1·8	41·2	0·4	39·6	0·9	1 226
1·7	0·7	34·9	0·4	–	–	–	–	35·0	1·7	–	–	34·2	1·5	631
0·9	0·5	41·8	0·3	41·0	1·5	–	–	44·0	1·2	–	–	42·8	0·5	758

sexes combined the weight data are shown in the upper diagram of Figure 6. As with length, the weight-at-age more or less remained constant until about 1963 and increased in all age-groups since 1964. The annual increments in weight also show a tendency to increase over the period but the major increase is again to be found in soles of three years old or younger. The increase in weight-at-age is most pronounced in the females (Fig. 7). From 1957 to 1973 the weight of four year old female soles in April increased from 200 g to 380 g, an increase of 90%; six year old females increased from 300 to 600 g, a 100% increase. Male soles increased some 50% in weight over the same 16 years. In order to exclude the length increment from the weight effect, changes in the condition factor have to be considered.

Variations in the condition factor

In sole the weight-length relationship can be described by $W = ql^a$, in which q is the condition factor[1]. In sole larger than 24 cm the exponent a equals 3, thus we use this value for our market samples. Table 4 gives the average condition factor for males and females per month and per year for gutted soles with gonads. Inspection of Table 4 reveals that the condition factor remained more or less constant from 1957–1963 and increased stepwise to a higher level

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[1] The condition factor usually given as k is here described as q to avoid confusion with the Von Bertalanffy coefficient of catabolism k.

Table 2. Average length ($\bar{l}$), standard error ($S\bar{l}$) and number of otoliths (n) used in length-age

Year	Sub-stock (see Fig. 3)		Age-group 3 $\bar{l}$	3 $S\bar{l}$	4 $\bar{l}$	4 $S\bar{l}$	5 $\bar{l}$	5 $S\bar{l}$	6 $\bar{l}$	6 $S\bar{l}$	7 $\bar{l}$	7 $S\bar{l}$	8 $\bar{l}$
1968	1	♂	25·9	0·3	27·4	0·3	29·2	0·4	–	–	–	–	35·2
		♀	27·0	0·3	31·8	0·3	33·8	0·3	–	–	–	–	38·9
	2	♂	25·9	0·3	27·2	0·2	31·5	0·4	–	–	–	–	–
		♀	29·6	1·2	31·5	0·3	34·3	0·2	–	–	–	–	39·1
	3	♂	26·8	0·3	29·2	0·3	29·8	0·2	–	–	–	–	31·0
		♀	30·4	0·5	33·0	0·5	34·2	0·2	32·7	1·8	40·3	0·6	36·7
1969	1	♂	25·9	0·1	28·7	0·3	29·6	0·3	30·5	0·3	–	–	–
		♀	27·6	0·2	31·4	0·4	33·8	0·2	34·4	0·3	–	–	40·9
	2	♂	25·6	0·1	27·1	0·3	29·2	0·3	30·4	0·3	–	–	–
		♀	27·7	0·2	32·4	0·4	34·2	0·3	35·2	0·2	–	–	37·6
	3	♂	27·4	0·2	27·9	0·5	30·3	0·3	30·5	0·2	–	–	–
		♀	28·9	0·4	32·9	1·3	34·8	0·4	35·7	0·2	37·1	0·7	–
	4	♂	25·9	0·2	28·4	0·5	29·2	0·3	31·1	0·3	–	–	–
		♀	27·7	0·2	32·5	0·5	33·3	0·3	35·6	0·2	39·3	0·6	–
	6	♂	26·7	0·2	30·7	0·6	31·5	0·4	32·0	0·2	–	–	–
		♀	30·0	0·5	33·1	1·3	33·5	0·4	34·8	0·3	–	–	–
1970	1	♂	27·5	0·2	29·4	0·5	31·3	1·0	31·9	0·4	32·6	0·2	–
		♀	29·1	0·2	32·5	0·5	36·3	0·8	34·5	0·4	37·1	0·2	35·1
	2	♂	26·5	0·1	28·0	0·2	29·0	0·8	31·2	0·4	31·8	0·3	–
		♀	28·5	0·2	32·2	0·2	34·4	0·5	35·6	0·5	37·4	0·2	–
	3	♂	27·5	0·1	30·2	0·4	29·8	0·6	31·6	0·5	32·0	0·2	–
		♀	29·7	0·2	32·9	0·3	34·0	0·8	36·4	0·5	37·1	0·2	41·5
	4	♂	26·9	0·2	29·0	0·3	32·1	1·0	31·8	0·3	33·1	0·3	–
		♀	28·5	0·1	30·8	0·3	34·2	0·5	36·5	0·4	37·2	0·2	–
	5	♂	27·7	0·2	28·6	0·4	31·4	0·7	30·6	0·6	30·6	0·2	–
		♀	30·2	0·3	33·6	0·9	36·1	1·0	36·3	0·6	37·3	0·3	–
	6	♂	27·7	0·2	28·8	0·4	–	–	31·8	0·6	32·8	0·2	–
		♀	28·7	0·2	31·9	0·6	33·3	0·6	35·3	1·4	36·7	0·2	36·5
1971	1	♂	27·9	0·3	29·9	0·3	31·2	1·0	30·7	0·8	34·1	0·4	34·2
		♀	28·9	0·3	33·6	0·3	34·9	0·4	37·1	0·9	37·5	0·9	39·0
	2	♂	27·7	0·2	29·7	0·2	31·1	0·3	29·9	0·7	32·7	1·0	33·1
		♀	29·5	0·3	33·7	0·2	35·2	0·3	37·7	0·4	38·1	0·4	38·6
	3	♂	28·0	0·2	30·5	0·2	31·9	0·4	31·2	0·6	34·0	0·5	33·3
		♀	29·2	0·3	33·7	0·2	34·9	0·9	37·6	0·6	37·6	0·5	38·8
	4	♂	27·2	0·3	28·9	0·4	29·2	0·8	31·0	0·4	32·6	0·3	33.5
		♀	28·9	0·4	32·8	0·6	–	–	36·2	1·3	37·3	1·2	40·8
	6	♂	27·9	0·3	30·2	0·3	31·4	0·8	32·8	2·0	32·0	0·4	33·9
		♀	28·4	0·2	30·1	0·4	32·9	0·6	34·1	1·3	35·9	0·6	37·1
1972	1	♂	27·2	0·2	30·9	0·4	32·6	0·4	33·4	0·6	–	–	34·4
		♀	28·9	0·2	33·2	0·5	36·5	0·4	37·5	0·3	39·6	0·5	38·7
	2	♂	27·4	0·1	30·2	0·6	31·4	0·4	33·7	1·3	–	–	–
		♀	29·7	0·2	34·1	0·3	36·5	0·3	38·5	0·6	38·5	0·5	40·3
	3	♂	28·0	0·1	30·0	0·5	32·4	0·5	33·5	0·7	–	–	32·6
		♀	29·7	0·1	33·0	0·4	36·2	0·4	36·6	0·8	–	–	38·9
	4	♂	27·9	0·1	29·5	0·4	32·1	0·3	33·1	0·6	–	–	35·2
		♀	29·2	0·3	33·2	0·5	35·7	0·4	39·4	0·7	38·3	0·7	38·7
	5	♂	28·5	0·2	30·1	0·3	30·7	0·4	31·4	0·7	–	–	33·0
		♀	30·3	0·3	33·1	0·4	35·0	0·6	36·8	0·6	39·6	1·0	38·3
	6	♂	28·1	0·1	31·1	0·1	33·1	0·4	33·7	0·7	34·6	1·0	35·4
		♀	29·3	0·2	32·0	0·5	37·0	0·5	38·0	0·9	38·9	1·0	–
1973	1	♂	27·9	0·3	29·5	0·3	31·2	0·3	33·3	0·6	31·9	0·3	–
		♀	31·2	1·1	33·9	0·5	37·3	0·7	38·3	0·4	39·2	0·4	39·9
	2	♂	27·1	0·2	29·6	0·3	31·8	1·0	32·4	0·9	33·1	1·2	33·1
		♀	30·3	0·4	34·2	0·3	36·2	0·6	39·8	0·5	39·9	0·7	41·3
	3	♂	28·2	0·2	30·6	0·2	31·0	0·5	32·5	0·4	33·9	0·4	–
		♀	30·0	0·3	33·8	0·2	35·7	0·7	38·2	0·5	40·5	0·8	39·1
	4	♂	28·2	0·3	30·5	0·2	–	–	32·9	0·8	–	–	–
		♀	30·7	0·6	34·7	0·3	37·4	0·5	39·5	0·4	39·4	0·8	40·5
	6	♂	29·4	0·5	31·7	0·4	32·2	0·4	35·2	1·3	–	–	–
		♀	30·2	0·3	34·2	0·4	34·6	0·8	35·2	2·1	–	–	–

various sub-stocks of North Sea sole in the second quarter, derived from market-sampling

9		10		11		12		13		14		15		Total number of otoliths (n) in length-age keys (including age-groups 15+)
$\bar{l}$	$S\bar{l}$	$\bar{l}$	$S\bar{l}$	$\bar{l}$	$S\bar{l}$	$\bar{l}$	$S\bar{l}$	$\bar{l}$	$S\bar{l}$	$\bar{l}$	$S\bar{l}$	$\bar{l}$	$S\bar{l}$	
–	–	34·0	0·9	–	–	–	–	–	–	–	–	–	–	68
8·0	0·9	40·4	0·4	–	–	43·6	0·7	39·2	1·2	41·0	0·3	–	–	109
–	–	33·3	0·6	–	–	35·7	0·4	–	–	–	–	–	–	138
–	–	40·6	0·2	–	–	42·6	0·8	–	–	–	–	–	–	152
–	–	31·7	1·1	–	–	32·6	1·4	–	–	–	–	–	–	194
–	–	37·4	0·7	42·9	1·0	39·9	0·6	–	–	–	–	–	–	239
3·5	0·9	–	–	34·2	0·9	–	–	–	–	–	–	–	–	223
7·8	0·7	40·7	0·7	41·1	0·2	41·1	0·3	44·0	0·9	45·8	1·7	43·0	1·0	307
–	–	–	–	33·4	0·5	–	–	–	–	–	–	–	–	197
0·4	0·6	39·5	0·0	41·7	0·4	40·1	1·4	42·6	0·7	–	–	–	–	285
–	–	–	–	33·4	0·9	–	–	–	–	–	–	34·4	2·4	218
0·6	0·5	42·0	1·4	39·1	0·7	–	–	43·3	0·9	–	–	–	–	244
5·3	1·2	–	–	36·0	0·4	–	–	–	–	–	–	–	–	120
–	–	–	–	40·7	0·4	–	–	40·7	0·5	41·9	0·4	–	–	205
1·8	0·4	–	–	34·1	0·3	–	–	32·6	0·6	–	–	32·9	0·8	176
7·5	0·6	37·2	1·1	38·2	0·4	43·0	0·5	41·0	0·8	–	–	41·7	0·8	207
–	–	34·9	0·9	–	–	34·8	0·3	–	–	34·0	0·4	–	–	238
–	–	39·7	0·5	–	–	37·6	0·5	42·3	2·0	40·8	0·9	41·4	1·1	281
–	–	33·4	0·5	–	–	34·4	0·6	–	–	–	–	–	–	250
–	–	39·7	0·5	–	–	42·0	0·3	–	–	42·1	0·9	42·0	0·8	357
–	–	–	–	36·5	0·7	34·3	0·7	–	–	32·0	0·4	31·8	1·1	248
–	–	37·4	0·9	–	–	39·4	0·5	44·0	0·4	40·1	0·5	42·0	1·0	308
–	–	–	–	–	–	36·2	1·4	–	–	–	–	–	–	186
–	–	39·0	0·8	–	–	39·9	0·3	–	–	39·6	2·0	41·8	0·7	336
–	–	33·0	0·6	–	–	32·5	0·6	–	–	32·7	1·7	–	–	146
–	–	–	–	–	–	41·2	1·0	43·0	1·5	42·0	0·4	–	–	144
–	–	33·8	0·7	–	–	32·2	0·4	–	–	–	–	–	–	238
–	–	39·4	0·5	38·7	0·8	40·2	0·3	39·8	1·5	42·8	2·0	43·2	1·2	314
–	–	–	–	–	–	–	–	35·9	0·8	–	–	–	–	191
–	–	–	–	39·8	1·7	–	–	39·5	1·0	–	–	–	–	237
–	–	–	–	–	–	–	–	37·3	1·1	–	–	–	–	235
–	–	–	–	41·3	1·0	–	–	42·4	0·4	–	–	41·7	0·8	247
–	–	–	–	–	–	–	–	34·8	0·6	–	–	–	–	268
–	–	–	–	–	–	–	–	40·8	0·6	–	–	–	–	342
–	–	–	–	33·9	0·7	–	–	–	–	–	–	–	–	89
–	–	–	–	–	–	–	–	42·5	1·0	–	–	–	–	111
4·7	0·7	–	–	35·0	0·2	–	–	37·0	0·1	–	–	–	–	242
–	–	–	–	37·5	0·2	–	–	39·1	0·1	39·7	0·4	39·0	0·3	344
5·1	0·3	–	–	–	–	–	–	–	–	37·8	0·5	–	–	250
0·5	0·3	–	–	–	–	45·9	1·2	–	–	43·3	0·5	–	–	273
4·7	0·4	–	–	–	–	–	–	–	–	35·9	1·5	–	–	213
0·6	0·3	–	–	–	–	39·5	1·2	–	–	37·8	2·3	–	–	271
4·0	0·5	–	–	–	–	–	–	–	–	–	–	–	–	257
0·3	0·3	–	–	–	–	41·5	0·5	–	–	42·0	0·5	–	–	376
5·2	0·2	–	–	–	–	35·4	0·5	–	–	36·8	0·5	–	–	243
1·3	0·4	–	–	–	–	–	–	–	–	43·0	0·7	–	–	170
2·8	0·3	–	–	–	–	–	–	–	–	33·3	1·7	–	–	200
8·7	0·3	–	–	–	–	39·9	0·4	–	–	41·4	1·6	42·5	1·4	156
4·6	0·3	–	–	–	–	33·7	1·0	–	–	36·1	0·4	–	–	258
9·9	0·3	40·8	0·9	40·8	1·1	38·9	1·5	40·3	1·7	41·5	0·4	39·6	0·9	310
–	–	32·5	1·1	–	–	–	–	–	–	–	–	–	–	77
2·2	0·3	42·5	0·7	–	–	–	–	–	–	–	–	–	–	64
–	–	33·8	1·8	–	–	–	–	–	–	–	–	–	–	112
2·0	0·4	43·3	0·6	–	–	–	–	–	–	–	–	–	–	136
–	–	34·4	0·5	–	–	–	–	–	–	–	–	–	–	229
1·9	0·4	41·6	0·4	–	–	–	–	45·6	0·7	42·4	1·3	43·0	0·6	312
1·7	1·4	37·5	0·7	–	–	33·5	–	–	–	–	–	–	–	151
7·7	1·0	40·9	1·1	41·0	0·4	43·5	–	–	–	–	–	–	–	95
–	–	36·4	0·5	–	–	–	–	35·0	0·4	–	–	34·2	0·3	75
0·6	1·5	40·9	0·5	–	–	–	–	42·3	0·3	–	–	42·5	0·7	171

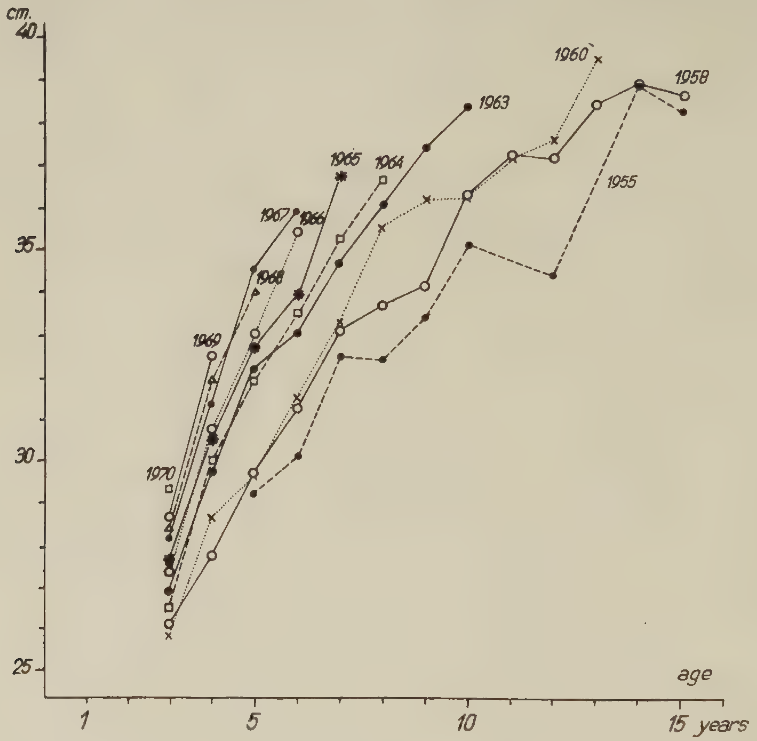

Figure 2. Average lengths for different year classes by age of North Sea sole, sexes combined, based on market sampling 1957–73.

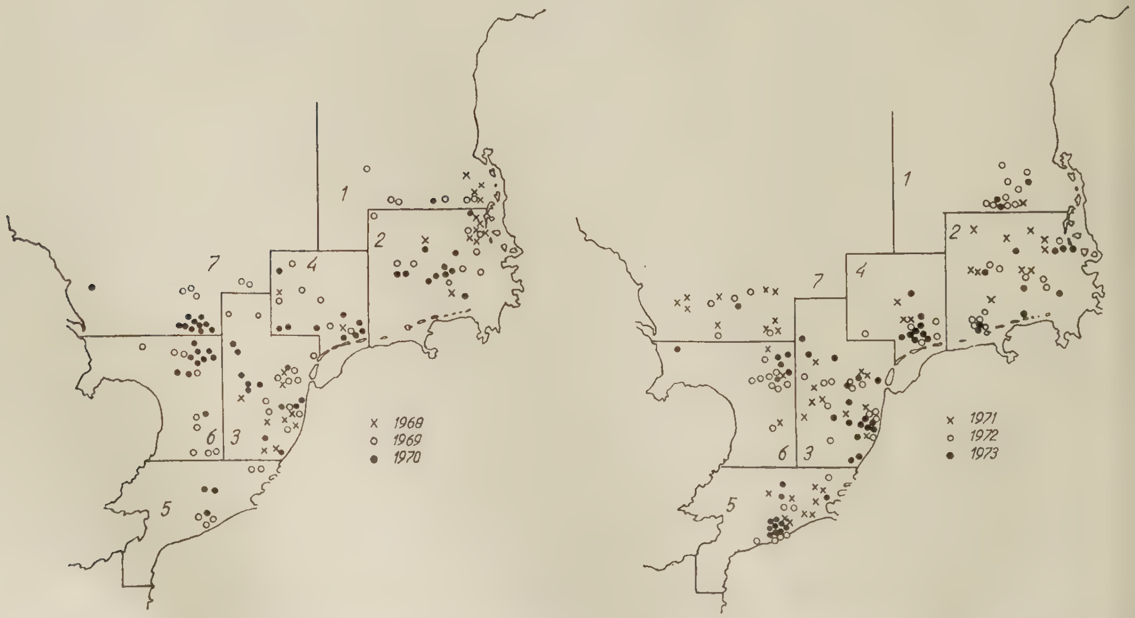
1
2
3
4
5
6
7
× 1968
○ 1969
● 1970
1
2
3
4
5
6
7
× 1971
○ 1972
● 1973

Figure 3. Positions of commercial ship samples in the second quarter 1968–1973; area-breakdown used for samplin defining sub-stocks.

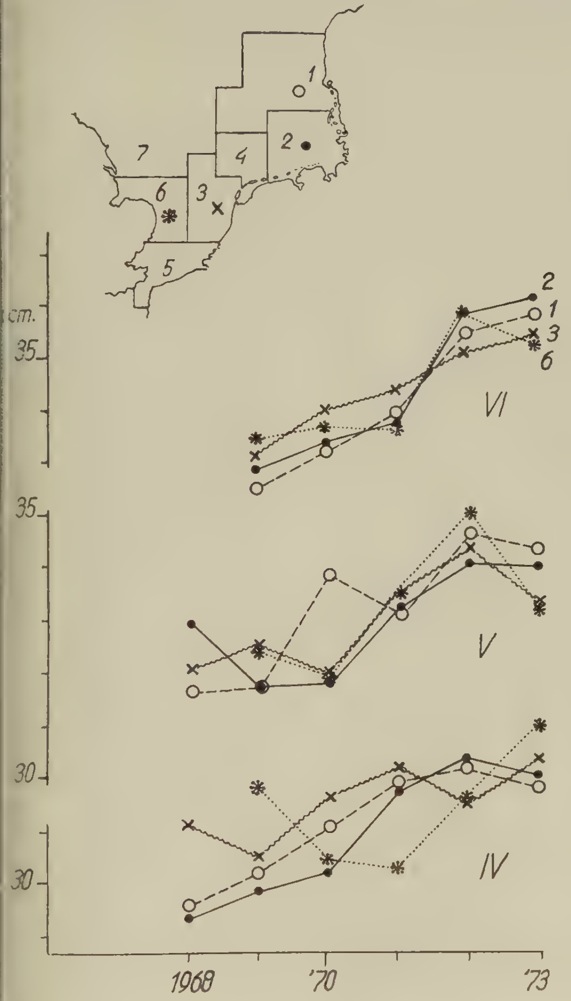

Figure 4. Average length in the second quarter for North Sea sole sub-stocks 1, 2, 3 and 6, sexes combined, in the period 1968–73.

in 1964. Since 1971 the annual condition factors are again at an even higher level. The amplitude of the monthly variation in the condition factor has also increased (Fig. 8). In 1957–1962 the amplitude in the condition factor of male soles was 10·7% of the minimum value in spring, but increased to 19% in 1968–1973. In females the amplitudes slightly increased from 15·8% to 16·5%.

Variations in the weight of the ovaries

Weighing ovaries on a routine basis was started in 1962. The weight of the ovary is a function of length, smaller soles having small and large soles having big ovaries. In order to compare variations in ovary weight of soles of different sizes, the weight of the ovary can be expressed as percentage of the gutted weight including gonads. This is shown in Figure 9 in which the monthly relative ovary weights have been given for four length groups. The diagrams show, that over the period concerned several changes have taken place.

Ovaries of soles of 25 cm developed to a weight of 5% of the gutted weight including gonads in 1962 but this decreased to some 1% in later years. This decrease in the relative weight of the fully developed ovary is also present in soles of 30 cm in which a change from 9% in 1962 to 5% in 1966 took place. Gonad weights of female soles of 35 cm remained constant and for soles of 40 cm they increased from 10% in 1962 to about 15% later on. These changes indicate that the relationship between relative ovary weight and length has become steeper and that this change took place in 1965–1966. In the following we will use ovary weight as an index of fecundity. In

Figure 5. Modal length of 0-group sole at the age of ½ and 1 year. Open circle 1913, from Tesch (1913) from Dutch coastal area; open circle 1934, from Bückmann (1934) from German coastal areas; black circles 1954–1967, from Meyer-Waarden and Tiews (1965), and Tiews (1971) from the German coastal areas; open circles 1969–1972, from Dutch Waddensea surveys; and crosses 1971–72 from De Clerck (1974) for the Belgian coast.

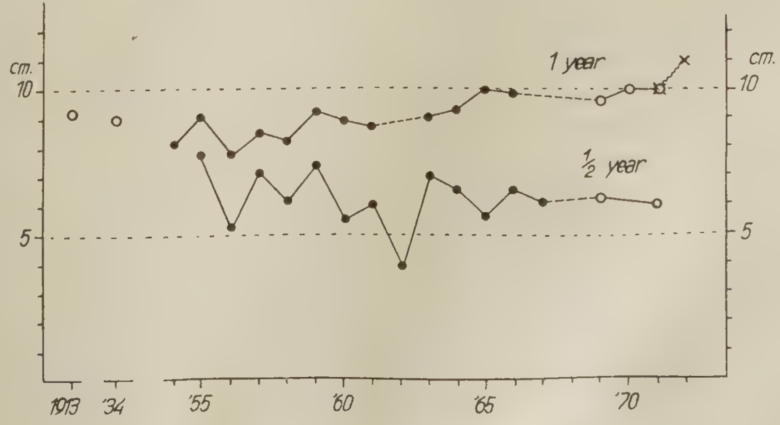

Table 3. Average gutted weight ($\bar{W}$) in g and number of otoliths (n) used in length-age key for North Sea sole in t

Year	Age-group	3*		4		5		6		7		8
		$\bar{W}$	n	$\bar{W}$	n	$\bar{W}$	n	$\bar{W}$	n	$\bar{W}$	n	$\bar{W}$
1957...	♂	118·1	7	129·8	12	178·4	5	203·0	9	192·9	18	234·0
	♀	135·3	23	184·6	41	251·4	10	295·2	13	339·7	32	440·0
1958...	♂	130·4	11	151·4	15	153·1	29	164·6	11	188·3	5	217·6
	♀	155·3	12	205·9	33	265·9	31	281·6	3	377·1	8	322·1
1959...	♂	125·4	7	128·0	9	154·1	9	177·1	7	170·7	1	240·5
	♀	152·8	18	200·2	27	275·8	29	299·0	13	373·8	3	407·9
1960...	♂	145·4	8	140·2	17	147·3	12	170·8	25	186·6	19	196·7
	♀	156·5	24	219·7	29	261·0	28	328·2	20	363·7	18	–
1961...	♂	123·6	20	176·2	3	155·7	9	155·7	11	216·8	15	188·3
	♀	140·1	63	249·9	28	262·1	28	270·9	23	329·6	15	367·2
1962...	♂	134·5	6	138·2	87	163·7	17	189·5	18	198·0	12	200·0
	♀	139·9	6	204·7	112	301·4	25	359·0	38	392·2	22	385·6
1963...	♂	119·6	10	146·5	14	157·3	134	164·6	30	191·1	22	188·9
	♀	144·2	39	188·1	21	266·3	132	309·6	34	340·4	29	382·0
1964...	♂	143·5	19	150·3	56	170·1	49	193·2	165	197·2	2	211·4
	♀	145·6	22	243·7	46	305·3	33	326·7	210	338·6	47	351·1
1965...	♂	136·8	3	195·7	16	176·2	16	219·5	9	250·5	55	207·4
	♀	195·6	4	231·9	5	280·8	15	338·0	12	384·9	65	393·5
1966...	♂	135·2	71	174·3	1	220·5	1	160·7	6	257·9	5	241·6
	♀	160·7	184	204·6	3	356·7	3	363·3	18	406·1	8	391·4
1967...	♂	124·1	68	169·3	271	197·4	6	211·3	3	214·2	13	192·9
	♀	165·6	79	250·8	391	240·4	9	427·1	5	409·4	48	452·5
1968...	♂	136·3	63	167·2	109	210·7	175	–	–	–	–	287·2
	♀	204·7	27	285·5	78	343·8	237	302·1	3	587·8	3	495·0
1969...	♂	141·5	261	185·3	80	212·0	152	237·8	352	–	–	252·2
	♀	191·7	259	306·2	76	347·5	169	388·3	438	511·9	12	518·8
1970...	♂	161·1	570	196·8	140	238·4	40	258·2	72	275·4	357	339·2
	♀	211·7	567	298·9	160	375·2	50	417·1	82	467·2	571	489·2
1971...	♂	183·1	245	234·2	243	274·4	89	205·6	14	327·7	39	329·9
	♀	225·7	272	338·2	250	391·1	69	505·3	25	485·1	53	547·7
1972...	♂	178·1	539	240·9	100	287·9	98	325·7	28	356·2	5	341·4
	♀	227·2	490	343·0	153	466·8	143	476·9	46	563·5	12	594·0
1973...	♂	183·9	177	227·8	281	255·5	38	316·8	23	293·9	10	299·8
	♀	249·7	147	366·7	246	436·1	55	528·8	49	592·2	25	628·5

* This age-group only partly recruited in the period 1957–1967 and average weight was thus assumed to be biase these years.

Figure 9 the role of the individual year classes is masked. It is possible to follow the year class influence by plotting the weights of the ovaries per year class.

Variations in ovary weight per year class

In Figure 10 the relationship between ovary weight in grammes and length per age-group is given for the month of maximum ovary development (April). Not all age-groups are represented every year owing to differences in year class strength. Thus the poorer year classes yielding too few points are omitted from the graphs. This figure shows that the change in fecundity took place rather abruptly from 1964 to 1965. The change affected all age groups at the same time. Apart from the change in the slope of the curves the already mentioned increase in length-at-age ca be observed in Figure 10 as a shift of the age grou curves to the right. The diagrams suggest that th change in fecundity is rather distinct. Except for th shift to the right the situation in April 1973 closel resembles that of 1966. The fact that all year classe demonstrated the change more or less in the sam year indicates that environmental rather than geneti factors are responsible.

A typical feature in Figure 10 is the fact that th year group curves do not fall on the same overlappin line, but that each year group has its own line, th relationship being fan-like in some years. This ma be the result of a small but continous increase in th ovary weight – age relationship. It may, however also mean that within one single year class the slo growing individuals develop ovaries too small fo their size and the fast growing soles ovaries of ex ond quarter derived from market sampling per age-group for males and females per year for the second quarter

9		10		11		12		13		14		15	
$\bar{W}$	n	$\bar{W}$	n	$\bar{W}$	n	$\bar{W}$	n	$\bar{W}$	n	$\bar{W}$	n	$\bar{W}$	n
62·5	13	257·7	22	292·1	1	–	–	472·8	1	–	–	–	–
48·7	12	467·5	47	580·6	1	644·6	3	691·7	2	707·1	1	423·0	2
53·4	10	224·6	5	242·4	21	–	–	–	–	–	–	415·8	1
62·3	15	482·1	6	516·4	43	600·5	1	478·3	1	600·5	1	–	–
21·9	8	196·1	2	261·8	1	256·3	2	–	–	–	–	–	–
41·0	7	483·3	9	485·4	8	512·9	18	456·7	2	641·0	2	–	–
–	–	227·6	10	445·5	1	220·7	1	278·0	12	–	–	–	–
89·4	5	522·2	18	477·4	10	472·6	6	609·0	25	–	–	–	–
74·5	3	234·5	4	250·2	5	330·6	2	327·3	4	369·1	8	–	–
34·6	10	388·5	5	434·8	16	487·0	12	256·0	3	530·4	28	–	–
73·6	7	243·8	1	236·0	4	219·6	5	288·7	5	339·3	3	363·8	10
80·2	15	510·2	3	476·4	14	656·1	10	580·5	15	656·1	6	620·1	34
20·5	10	210·6	5	268·5	3	283·6	6	303·7	3	303·7	3	311·8	2
15·6	13	479·6	15	516·2	5	–	–	604·5	16	512·3	2	588·6	3
29·0	8	277·9	4	277·9	4	320·3	2	385·2	5	251·7	4	330·2	2
00·6	21	467·7	31	413·7	19	497·3	4	490·8	15	508·4	11	629·0	18
–	–	263·2	3	–	–	263·2	4	315·6	2	335·9	2	377·2	1
98·2	8	519·9	4	450·9	6	657·9	8	459·3	3	–	–	647·6	3
20·5	1	254·2	5	470·8	1	–	–	264·4	3	–	–	374·5	1
09·9	11	417·7	18	613·0	9	479·4	17	668·9	5	536·8	1	701·7	2
39·3	31	–	–	234·0	5	211·3	3	277·3	3	291·3	4	–	–
31·1	149	431·1	11	499·6	19	488·1	7	530·3	25	601·7	15	611·2	3
–	–	284·3	18	–	–	315·6	6	–	–	–	–	–	–
86·2	2	553·4	83	701·9	6	662·4	14	540·3	2	618·9	3	–	–
98·7	22	408·5	1	324·8	43	408·5	1	304·2	7	304·2	4	344·7	6
38·0	54	557·0	14	582·7	153	561·3	10	681·2	28	781·5	7	781·5	12
96·1	2	304·3	24	366·0	5	326·3	61	379·9	5	280·6	12	342·1	4
05·3	2	538·6	41	523·4	9	581·6	175	702·8	14	625·2	27	657·9	23
–	–	–	–	374·5	14	–	–	431·3	35	–	–	–	–
–	–	–	–	583·6	18	–	–	642·1	84	–	–	610·9	13
73·0	130	–	–	–	–	461·6	12	–	–	470·7	29	–	–
40·8	209	–	–	–	–	862·0	16	518·7	3	669·0	73	809·2	7
50·1	6	348·4	35	–	–	–	–	341·1	2	–	–	328·6	2
23·4	23	676·7	84	697·8	2	–	–	755·0	7	747·4	2	712·7	24

cessive weight. Very probably it is the last assumption which is correct.

When ovary weight in April per year class is plotted against age (Fig. 11) it is obvious that the number of years needed to reach, for example an ovary weight of 100 g, has decreased since 1962. It took the 1965 and 1966 year classes only 7 to 8 years to achieve this, whereas the 1963 year class reached this level after 8–9 years. For the 1958 year class the interval was 12–13 years. Older year classes needed even more than 15 years to attain the 100 g level. If ovary weight can be taken as an index for fecundity, as has been proved for the lemon sole (Newton and Armstrong, 1974), the observed increase in gonad weight-at-age undoubtedly will influence the egg-production of the sole stock.

Earlier the condition factor was considered in relation to gutted weight including gonads. The observed increases might be completely due to the increase in ovary weight. This cannot be checked for the males because of lack of information on male gonad weights. For the females the somatic gutted weight can be calculated by subtracting ovary weight from gutted weight including gonads. Thus the annual weight increment per age can be split into a somatic and a reproductive component. In Figure 12 the annual increments by age determined from April to April are given for four periods for somatic tissue weight (hatched columns) and reproductive tissue weight (black columns). With increasing age less weight increment goes to somatic tissue and more to reproductive tissue. The ratio of somatic to reproductive increment is 1:1 at about 7–8 years of age. Both somatic and reproductive increments increased over the period and, therefore, the changes in total weight mentioned before are not restricted to the gonads

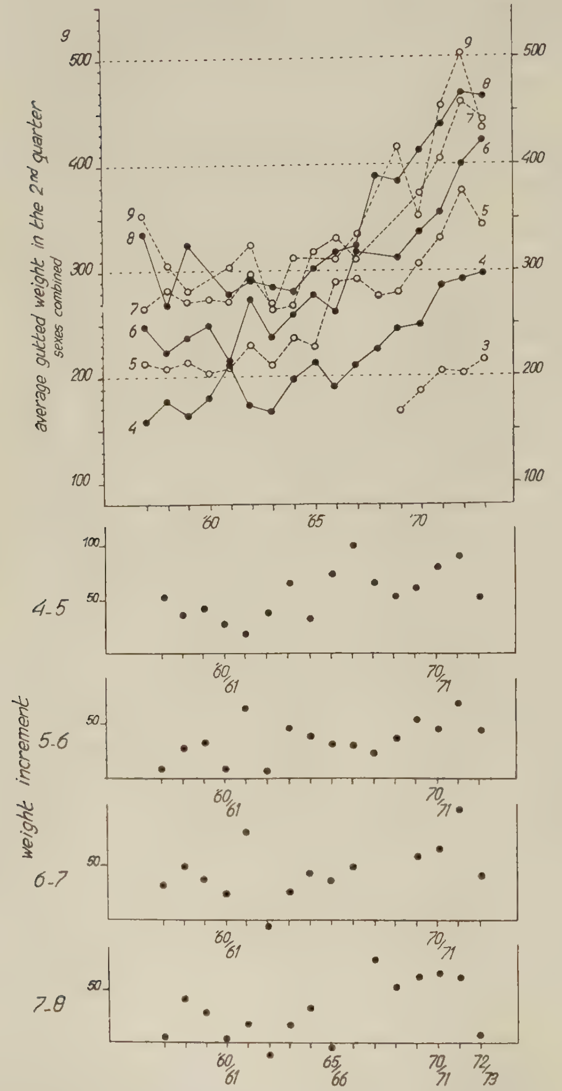

Figure 6. Top diagram, average gutted weight-per-age for North Sea sole with gonads, sexes combined, in the second quarter, based on market sampling 1957–73: other diagrams, annual weight increments by years.

only. It is not clear, whether the point of equal increment in both components changed from 1962–1964 to 1971–1973 owing to the large variations in the data.

Changes in recruitment to the spawning stock

The maturity – length ogive for female soles can be derived from the monthly data on maturation collected since 1964. The criterion used is that mature female soles must have reached at least stage 4 in May and June. I have shown (de Veen, 1970) that the gonads of age-group II may develop in May up to stage 3 but stop developing further in June. These soles are not considered to be mature for the present calculations. De Veen (1970) demonstrated that in the period 1964–1969 the length at which 50% of the females mature – the 50% point of the maturity ogive – was 27·5 cm for North Sea sole. Compared with the data for North Sea sole given by Holt (1892) and Bückmann (1934) this value appeared to be remarkably constant over a long period, Holt's 50% length being 27·5 cm and that given by Bückmann 27·2 cm.

Very recently, however, this picture changed. In 1969 the ogive was raised by some 2·5 cm and this remained so in the following years. Figure 13 gives the annual ogives in which the data for the years 1964 and 1965 were pooled for lack of sufficient data in the ogive length range owing to poor year classes. The diagrams show clearly the shift to the higher level in 1969. Figure 14a gives the 50% points of the ogives of Figure 13 together with the values given by Holt and Bückmann. Figure 14 b shows the average maturity – length ogives for 1964 to 1968 and for 1969 to 1973. In the preceding section fecundity was shown to have started to change in 1965 and we have just discussed an abrupt change in maturity – length in 1969, 4 years later. It might be possible that the change started with one particular year class which was born for example in 1966 and matured for the first time in 1969. We have to consider therefore the 50% lengths of the ogives per age-group.

From Figure 15 it is evident that the 4 year old and the 3 year old soles simultaneously changed their maturity-length relationship in 1969 and the conclusion must be drawn that an unknown factor affected the maturity – length relationship of all year classes in one particular year, 1969. The other diagrams in Figure 15 give the average ogives for 1964–1968 and for 1969–1973 for the age-groups 3, 4 and 5 and older. The change in the 50% length is greatest in the 3 year old soles, nearly 3 cm, whereas in the 5 year and older fish the change is less than 2 cm. Another feature is the increasing steepness of the ogives with age, which has not been affected by the change.

Did the change in the maturity – length relationship take place in the whole North Sea stock to the same extent or are there differences between the sub-stocks? Figure 16 gives the answer to this question. Apparently the distinct change in 1969 took place in sub-stocks 1, 2 and 3 and probably in sub-stocks 4 and 5, although no complete data are available. For sub-stock 6 only data for 1969, 1970, 1972 and

Table 4. Average condition factors ($q \times 10^2$) of gutted North Sea sole

					Males							
Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Aver. year
1957....	0·8208	0·8405	0·8090	0·8035	0·7749	0·6994	0·8209	0·8810	0·8669	0·8729	0·8372	0·8423	0·8224
1958....	0·8295	0·8649	0·8155	0·7717	0·8150	0·7299	0·6814	0·7118	0·8033	0·7524	0·8172	0·8507	0·7869
1959....	0·7777	0·7640	0·7992	0·8076	0·7419	0·7720	0·8222	0·8485	0·8055	0·8169	0·8629	0·8428	0·8051
1960....	0·8192	0·8386	0·7668	0·8166	0·7953	0·8040	0·7699	0·7708	0·7411	0·8017	0·8012	0·8173	0·7952
1961....	0·8045	0·7718	0·8280	0·7840	0·8081	0·7349	0·7829	0·7754	0·7571	0·8093	0·8236	0·8140	0·7911
1962....	0·8617	0·8959	0·8351	0·8238	0·7742	0·7958	0·7494	0·7569	0·7602	0·8419	0·8695	–	0·8149
1963....	0·8848	0·7832	0·7872	0·7743	0·7920	0·7176	0·7378	0·7857	0·8135	0·8548	0·8785	0·8986	0·8090
1964....	0·8791	0·8516	0·8496	0·8055	0·8156	0·7493	0·8375	0·8344	0·8937	0·8839	0·8963	0·8983	0·8496
1965....	0·9475	0·8724	0·8867	0·8689	0·8568	0·7840	0·7932	0·8342	0·8982	0·8762	0·8936	0·8590	0·8642
1966....	0·8779	0·8910	0·7897	0·7412	0·8029	0·7927	0·8361	0·8130	0·8350	0·8801	0·8407	0·8866	0·8322
1967....	0·8091	0·8691	0·7792	0·8084	0·7484	0·7945	0·7670	0·8178	0·9020	0·8822	0·8960	0·8649	0·8284
1968....	0·8926	0·8894	0·7963	0·7782	0·7751	0·7399	0·8076	0·7720	0·9162	0·8801	0·8929	0·9025	0·8369
1969....	0·8625	0·8215	0·7721	0·8094	0·8213	0·8118	0·7001	0·7855	0·8958	0·9010	0·9101	0·8802	0·8309
1970....	0·9072	0·8485	0·8158	0·8267	0·7846	0·8221	0·7588	0·8624	0·9224	0·8320	0·8869	0·8606	0·8440
1971....	0·9236	0·8927	0·8434	0·8947	0·8665	0·8925	0·8233	0·9026	0·9424	0·9107	0·9104	0·9575	0·8967
1972....	0·9376	0·9583	0·9004	0·9073	0·8506	0·8306	0·8410	0·7703	0·9370	0·9151	0·9243	0·8729	0·8871
1973....	0·8720	0·8493	0·9156	0·8659	0·8078	0·7872	–	0·8531	0·9520	0·9503	0·9478	0·8654	0·8788

					Females							
Year	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Aver. year
1957....	0·8930	0·9329	0·9388	0·8997	0·8125	0·7588	0·8317	0·8850	0·9036	0·9538	0·8981	0·9222	0·8858
1958....	0·9320	0·9747	0·8865	0·8626	0·9053	0·7791	0·7432	0·7857	0·8319	0·8379	0·8859	0·9091	0·8612
1959....	0·8784	0·9039	0·9099	0·8983	0·8779	0·8177	0·8358	0·8213	0·8356	0·9118	0·8899	0·9735	0·8795
1960....	0·8997	0·9287	0·9167	0·9139	0·8378	0·8138	0·8045	0·8112	0·7985	0·8548	0·8762	0·8773	0·8611
1961....	0·8838	0·8883	0·9011	0·8431	0·8159	0·7652	0·7932	0·8296	0·8379	0·8848	0·8796	0·8761	0·8499
1962....	0·9443	0·8756	0·9315	0·9415	0·9041	0·7985	0·7674	0·8157	0·7865	0·8594	0·8902	–	0·8646
1963....	0·9403	0·8924	0·8733	0·9200	0·8204	0·7899	0·7373	0·8179	0·8284	0·8834	0·9272	0·9448	0·8646
1964....	0·9393	0·9298	0·9422	0·8765	0·8419	0·8101	0·8599	0·8396	0·8912	0·9117	0·9421	0·9664	0·8958
1965....	1·0540	0·9566	0·9774	0·9497	0·9241	0·8205	0·8308	0·8370	0·9180	0·9105	0·8880	0·9277	0·9162
1966....	0·9311	0·9315	0·8914	0·8318	0·8645	0·8252	0·8606	0·8622	0·9195	0·9083	0·9358	0·9313	0·8911
1967....	0·8901	0·9245	0·8576	0·8951	0·8228	0·8176	0·8152	0·8724	0·9776	0·9543	0·9741	0·9194	0·8934
1968....	0·9778	0·9710	0·9500	0·9016	0·8510	0·7929	0·8655	0·8077	0·9311	0·9288	0·9765	0·9685	0·9102
1969....	0·9338	0·9199	0·9440	0·9243	0·8758	0·8444	0·7435	0·8387	0·9735	0·9641	0·9687	0·9893	0·9100
1970....	0·9831	0·9614	0·8794	0·8924	0·8585	0·8413	0·8103	0·8760	0·9412	0·9143	0·9854	0·9680	0·9093
1971....	0·9995	0·9870	0·9750	1·0352	0·9724	0·9159	0·8623	0·8949	0·9695	1·0031	1·0166	1·0013	0·9694
1972....	1·0669	1·0455	1·0897	1·0044	0·9330	0·8672	0·9789	0·8670	0·9003	0·9404	1·0226	0·9984	0·9762
1973....	0·9897	1·0040	1·0219	0·9963	0·9141	0·8543	–	0·9000	0·9673	0·9981	0·9895	1·0205	0·9687

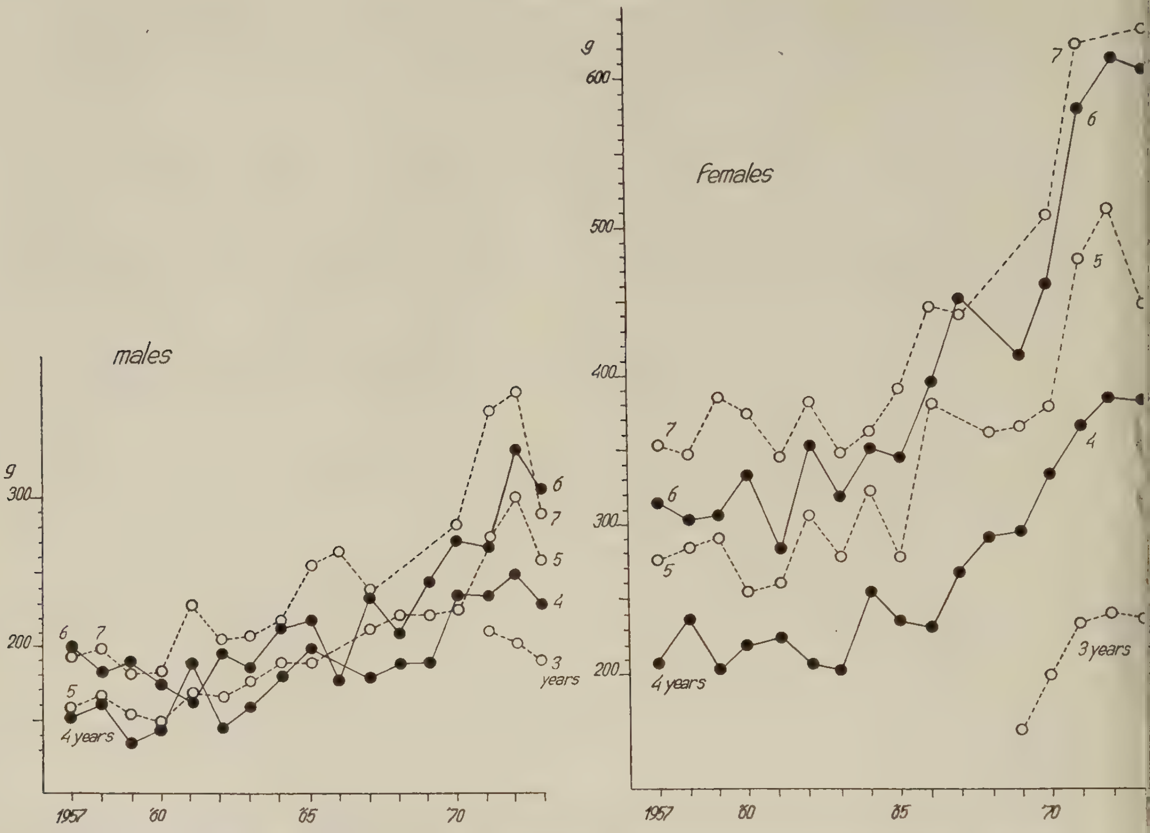

Figure 7. Average gutted weight-per-age of male and female North Sea sole with gonads in April by years.

1973 are present, which are all in line with the higher level of 50% lengths of the other sub-stocks. Apparently the change in 1969 affected all sub-stocks to the same extent and the factor responsible is not restricted to parts of the central or southern North Sea but covers the whole area.

Changes in recruitment to the spawning stock as a function of age

In the preceding section the maturity – length relationship was discussed. Reaching maturity for the first time is not only a matter of length but also of age. In Figure 17 the maturity ogives for female soles are given per year as a function of age. The 50% ages of the ogives are shown in the lower right hand corner. In contrast to the length ogives which changed to another level in 1969, the age ogives give a more complex figure. In the years 1966–1970 the 50% age increases but falls in 1971. The 50% age for 1964–1965 is higher than that in 1966. There is variatio around a constant level, which is about 3·2 years

Each ogive contains several year classes. In orde to find out what the effect per year class is, maturity age ogives were constructed per year class (Fig. 18) From this diagram the same conclusion can b drawn as from Figure 17: variation around a constan level of 3·2 years.

Unfortunately data on maturity – age for Holt' and Bückmann's prewar ogives are not availabl because there was no reliable age determination i their periods. Thus there is no indication that age a first maturity is influenced by the factors responsibl for the other changes in biological parameters tha have been discussed.

Variations in the Von Bertalanffy growth parameters

The Von Bertalanffy growth parameters L_∞, W K and t_0 were calculated from Table 1 and the ave

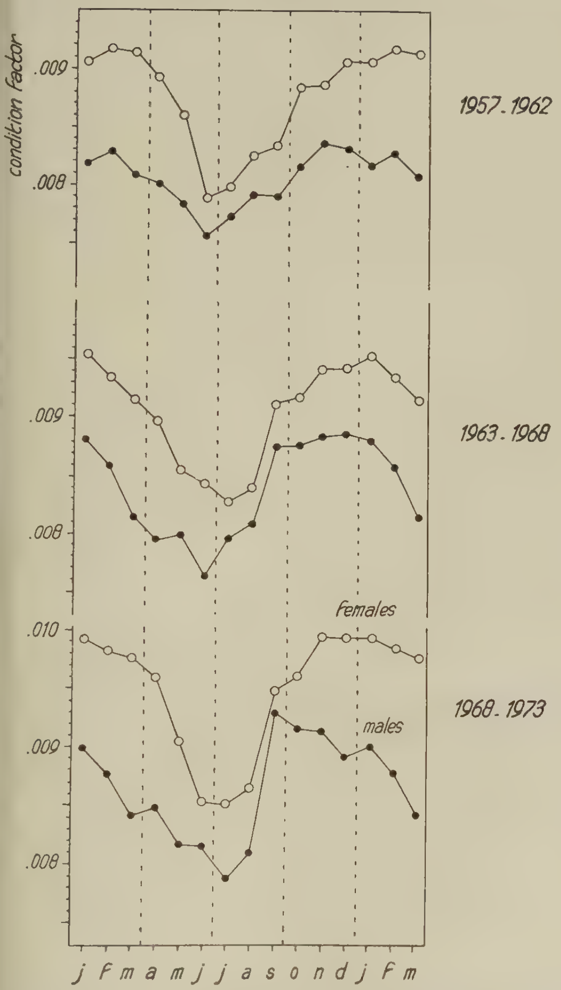

Figure 8. Average condition factor for males and females with gonads per month for the periods 1957–62, 1963–68 and 1968–73.

age annual condition factors calculated for the sexes separately. In order to determine L_∞ and K the functional or geometric mean regression of L_{t+1} over L_t has been calculated (Ricker, 1972, p. 412). Table 5 summarises the annual growth parameters.

Both L_∞ and W_∞ show an increase which is significant for both sexes ($P < 0{\cdot}01$, Spearman's rank correlation coefficient). But K as well as t_0 tend to decrease. However, the decrease in these parameters is only probably significant ($P = 0{\cdot}02$) for females and is not significant for males.

Another way of expressing growth is to use the Von Bertalanffy equation in its original form:

$$dW/dt = HW^{2/3} - kW^n$$

where $HW^{2/3}$ is the anabolic and kW^n the catabolic term, as has been discussed by Nielsen (1973). It should be noticed that the catabolic coefficient k is *not* identical to the Von Bertalanffy growth parameter K.

The observed annual increment in weight ΔW depends largely on the season or month in which it was determined owing to fluctuations in weight-at-age throughout the year. The Von Bertalanffy approach does not take account of this seasonal fluctuation but assumes continuous growth throughout the year.

In Figure 19 the average monthly gutted weight including gonads and the weight of the ovary (in black, and repeated separately on a larger scale at the bottom of the Figure) are given for North Sea sole as a function of age. It is based on data from 1962–1973. Although the seasonal variation in gutted weight including gonads increases with age there is a strict timing of the curves for each age. Somatic weight reaches its maximum around the 1 of January and ovary weight in March–April. Reproductive tissue appears to be formed at the expense of somatic tissue each year. The seasonal variation in somatic and reproductive weight is very regular.

It is reasonable to assume that we may use the data from corresponding months to estimate ΔW, so that we calculate the weight increment from January to January in the next year, February to February and so on. This results in 12 estimates per age group per year. The calculations were made for females only in order to see whether this method of analysing growth would yield results which are better interpretable than determining L_∞, W_∞, K and t_0.

The equation

$$dW/dt = HW^{2/3} - kW^n$$

can be written as

$$dW/dt = HpL^2 - kqL^{3n} \text{ with } n = 1$$

in which p is a physiological factor equal to $q^{2/3}$ and q is the condition factor.

Monthly condition factors have been tabulated in Table 4. The length value in the equation is the average between the length at the beginning and at the end of the 12-month period concerned:

$$(L_{ij} + L_{ij+1})/2$$

in which i stands for month and j for year.

The coefficients H and k were determined by least squares regression of

$$\Delta W_{ij} = a_{ij}L^2_{ij} + b_{ij}L^3_{ij}$$

in which $a = Hp = Hq^{2/3}$ and $b = -kq$.

Table 6 and Figure 20 give the annual average estimates of H and k for the years 1957–1973. The coefficient of anabolism H is more or less constant from 1957 to 1964, thereafter rising to a higher level.

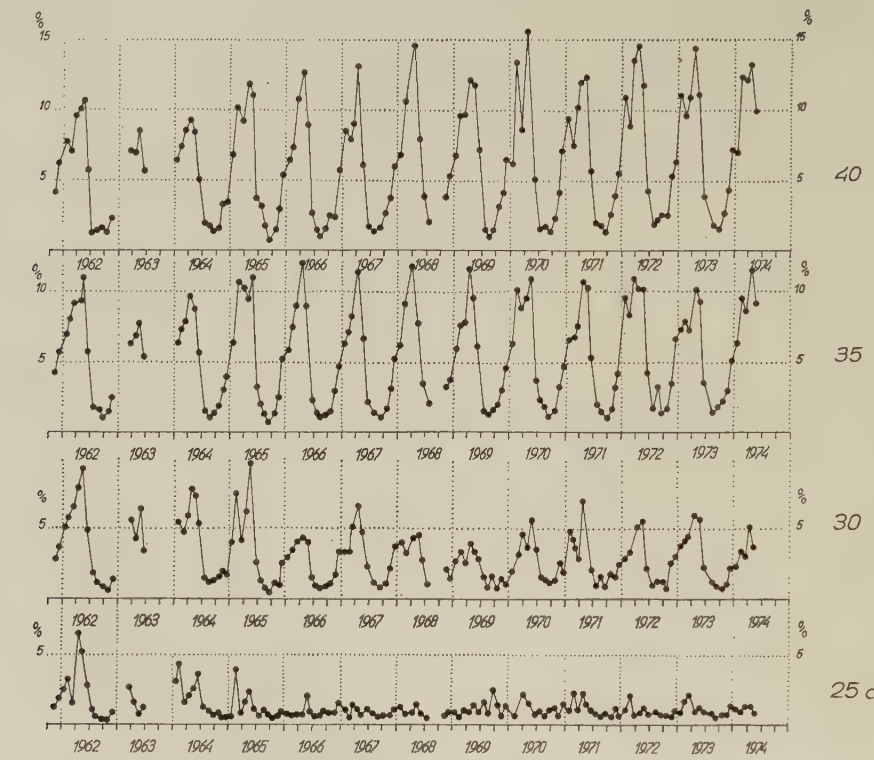

Figure 9. Relative weight of female gonads (as % of gutted weight including gonads) per month for the years 1962–74 for 4 length categories.

Table 5. North Sea sole: the Von Bertalanffy growth parameters estimated for the years 1958–1973

Year	L_∞ cm		W_∞ g		K		t_0 years	
	♂	♀	♂	♀	♂	♀	♂	♀
1958............	30·2	35·6	217·4	387·6	0·393	0·380	−2·0	−0·
1959............	29·9	36·9	215·0	441·2	0·377	0·362	−2·1	−0·
1960............	31·2	39·3	241·1	525·5	0·180	0·339	–	+0·1
1961............	24·5	35·0	–	364·1	−0·582	0·495	–	+0·1
1962............	30·1	38·5	222·5	492·3	0·289	0·503	−4·2	+1·
1963............	32·0	36·6	265·6	424·6	0·378	0·230	−0·7	−3·
1964............	33·0	38·1	305·0	493·5	0·415	0·394	+0·04	+0·
1965............	31·6	38·6	274·0	526·5	0·337	0·437	−2·1	+0·
1966............	28·2	38·0	–	490·1	−0·252	0·425	–	−0·1
1967............	30·7	38·4	240·3	505·9	0·556	0·306	−0·8	−1·
1968............	19·6	46·5	–	915·2	−0·279	0·230	–	−0.
1969............	33·5	41·7	311·3	658·0	0·302	0·213	−2·3	−2·
1970............	34·2	39·6	337·6	521·5	0·359	0·352	−1·3	−0·
1971............	36·2	40·2	424·0	629·8	0·294	0·286	−1·7	−1·
1972............	36·9	46·6	445·4	867·8	0·282	0·255	−2·3	−1·
1973............	33·9	44·4	340·9	846·2	0·353	0·264	−3·2	−1·

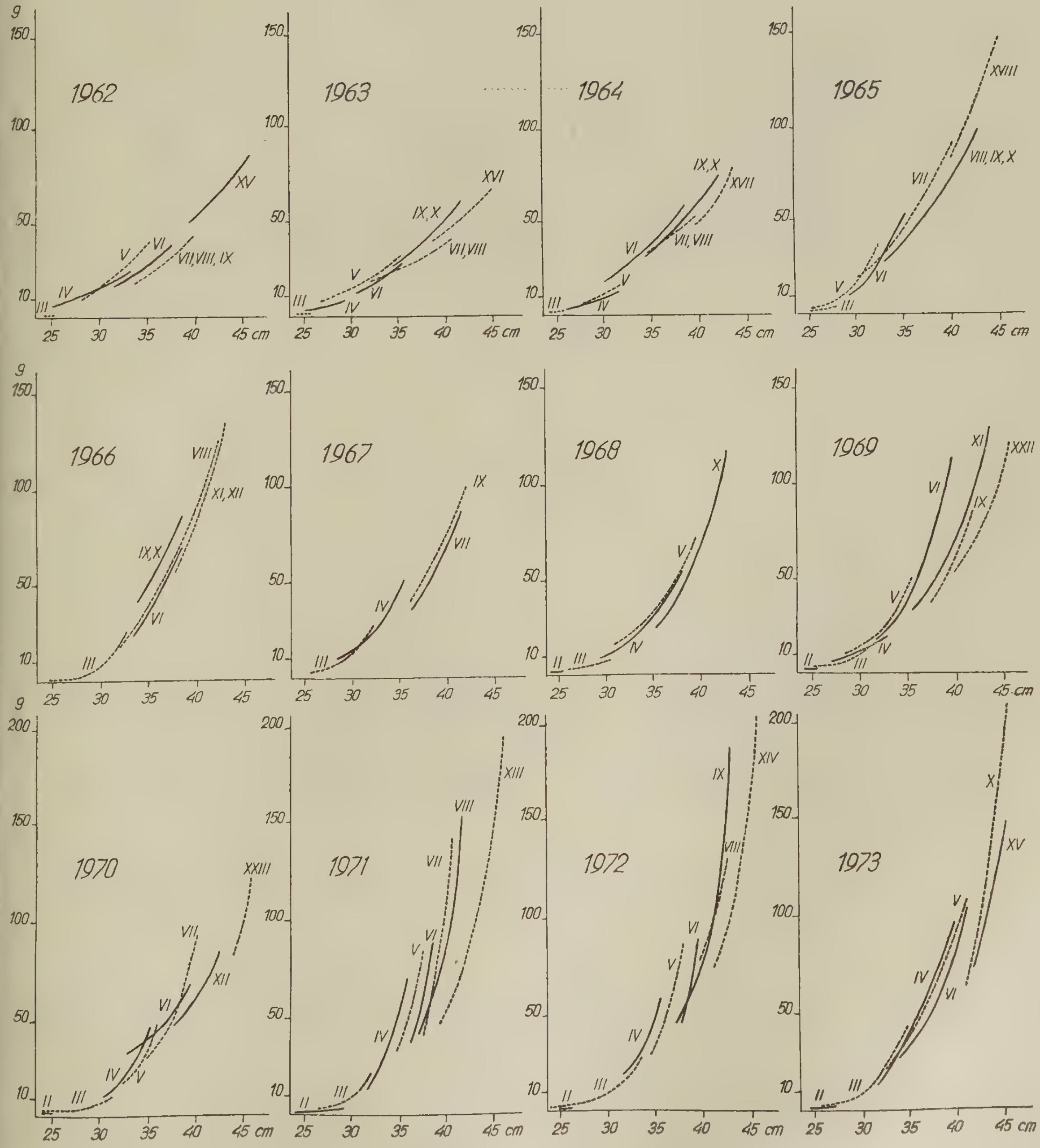

Figure 10. Relationship between female gonad weight per age-group and length for the years 1962–1973.

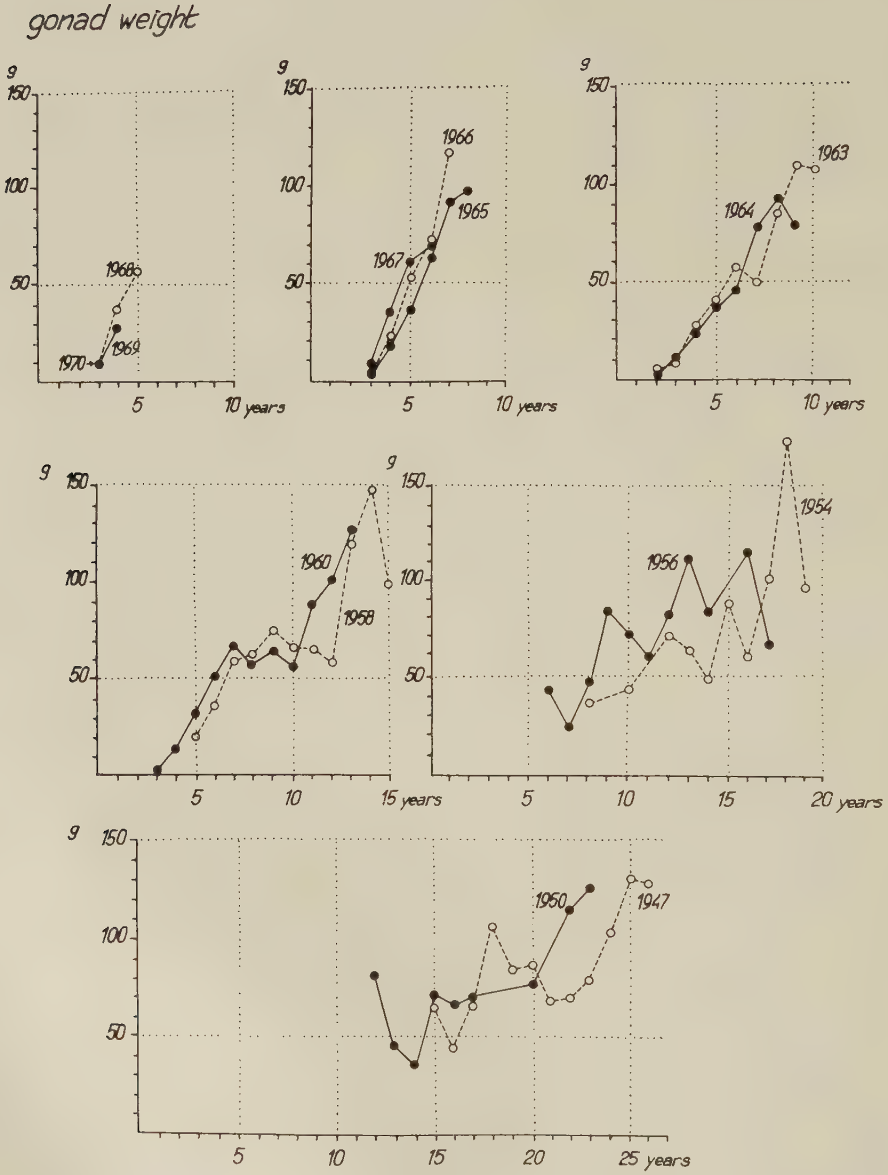

Figure 11. Relationship between female gonad weight per year class and age for a number of year classes.

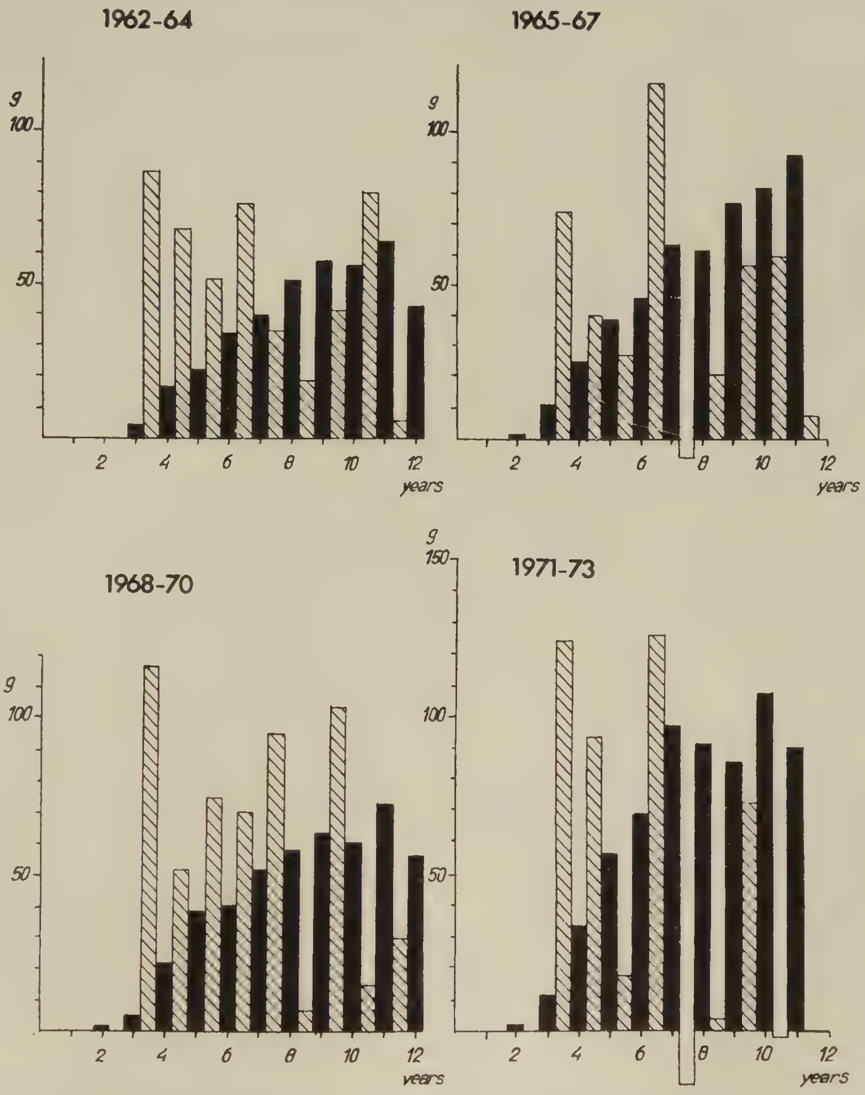

Figure 12. Annual increments in somatic weight (hatched) and female gonad weight (black) per age for the periods 1962–64, 1965–67, 1968–70 and 1971–73.

The coefficient of catabolism follows the same trend as H. When comparing the W_∞ estimates with those of H it is apparent that both show the same trends.

Correlations of the observed changes in biological parameters with the environment

Comparison of the observed changes in the sole stock with indices of the environment might give some insight as to the possible underlying factors. However, a correlation by itself does not prove that a relationship is causal and we have to look for additional evidence for direct causal factors.

The first possibility to be considered is a density dependent mechanism in growth. By means of Virtual Population Analysis (Gulland, 1956) the total number and total weight of the sole stock has been calculated per year (VPA, de Veen, 1974 unpublished; ICES, 1975). One year old soles were excluded for occupying different areas than older fish. Thus the sole stock was assumed to consist of 2–15 year old fish. Stock densities in number and weight were cal-

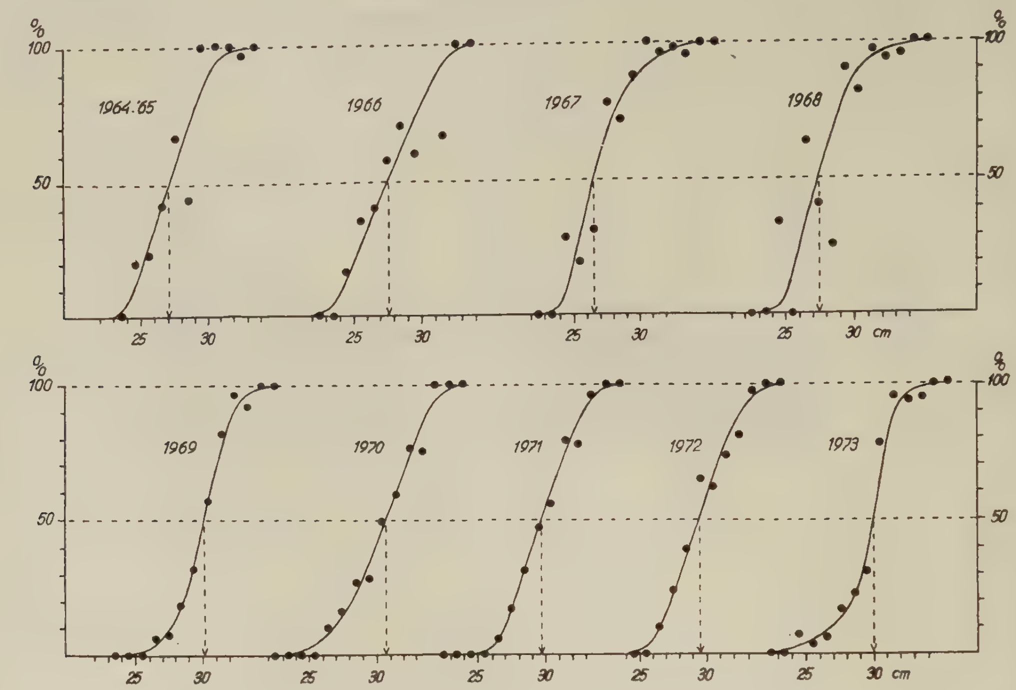

Figure 13. Maturity-ogives in May–June for female soles reaching at least stage 4, by years against length.

Table 6. Average annual coefficients of anabolism (H) and catabolism (k) for female North Sea sole.

Year	Coefficient of anabolism (H)	Coefficient of catabolism (k)
1957/58..........	5·98	0·65
1958/59..........	5·55	0·94
1959/60..........	6·15	0·89
1960/61..........	6·18	0·75
1961/62..........	4·26	0·68
1962/63..........	4·48	0·45
1963/64..........	6·31	0·64
1964/65..........	3·12	0·30
1965/66..........	10·66	1·20
1966/67..........	9·90	1·15
1967/68..........	9·24	1·07
1968/69..........	14·34	1·67
1969/70..........	6·84	0·77
1970/71..........	18·03	2·08
1971/72..........	17·76	1·98
1972/73..........	8·33	1·07

culated for the sexes separately. Table 7 gives the data for the sexes combined. We have found that the changes in growth were mainly apparent in 2 and 3 year old soles. Stock density in number and weight was therefore calculated for these two age groups alone.

A second possibility is the influence of temperature on growth phenomena (Weatherly, 1972). A difficulty is that there is no long term series of observations of bottom temperatures representative for the whole area occupied by the North Sea sole. The best data

Table 7. North Sea sole. Stock size in numbers and gutted weight of 2–15 year old fish and of 2 and 3 year old fish for 1 July derived from Virtual Population Analysis with $M = 0{\cdot}10$

Years	2–15 years stock size in numbers $\times 10^{-8}$	2–15 years stock size in weight $\times 10^{-5}$ kg	2+3 years stock size in numbers $\times 10^{-5}$	2+3 years stock size in weight $\times 10^{-6}$ kg
1957...	4 228	80·0	1 807	17·5
1958...	4 821	90·5	1 963	19·0
1959...	6 345	110·4	2 275	21·9
1960...	7 300	126·0	4 771	50·8
1961...	6 515	126·5	3 787	49·2
1962...	5 333	120·2	1 073	11·9
1963...	3 914	101·0	825	12·6
1964...	5 334	108·8	389	6·0
1965...	8 113	135·6	6 131	69·8
1966...	7 759	145·0	6 691	90·1
1967...	6 521	150·9	1 836	24·6
1968...	5 196	136·7	1 240	18·6
1969...	4 064	109·7	1 596	20·9
1970...	3 596	99·7	1 410	23·4
1971...	3 518	99·4	1 959	31·9
1972...	3 069	89·5	1 901	36·3
1973...	2 628	84·6	1 156	18·8

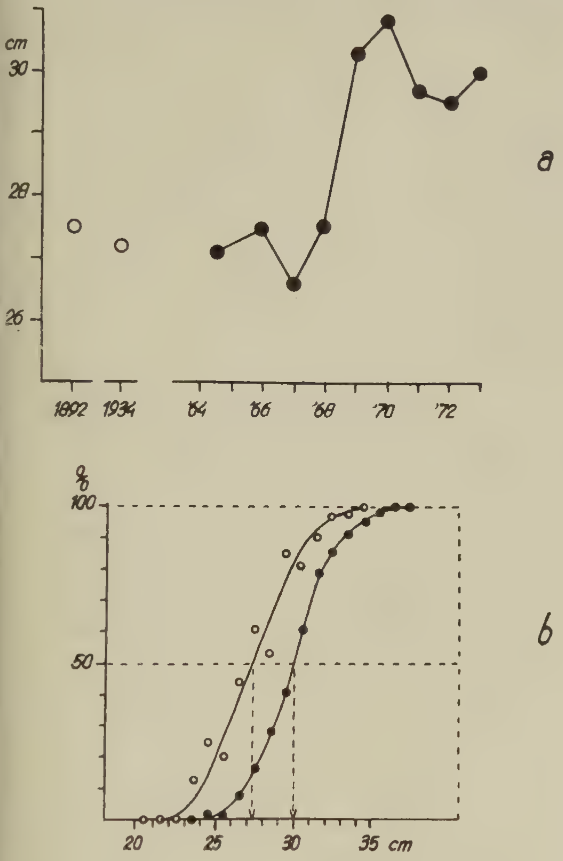

Figure 14. a, The 50% points of the ogives of Figure 13 together with Holt's (1892) and Bückmann's (1934) 50% length, by years; b, average maturity ogives for 1964–68 (open circles) and 1969–73 (black circles) against length.

available were the series of monthly surface water temperatures collected at the light-vessels "Vyl" and "Texel". From the combined data the number of days with temperatures above 14°C and above 15°C have been calculated together with the average August + September surface temperatures in the period of rapid growth of the sole. These data are given in Table 8.

Another important factor might be the average density of bottom animals serving as food for soles. The sole is a typical polychaete – molluscs feeder, searching for food in the night using olfactory stimuli (de Groot, 1971). No long term series of bottom fauna densities in the North Sea, representative for the sole area, exists, thus making it impossible to study this essential possibility.

It is a fact that eutrophication takes place in the North Sea. This might result in a richer supply of food animals. The major source for this eutrophication in the southern and central North Sea is the river Rhine. Unfortunately no long term series of, for example total phosphate in the coastal areas exists. Instead of total P a series of observations on orthophosphate in the Dutch part of the river Rhine (van Bennekom, Gieskes and Thijssen, 1975) from 1957 to 1970 was used as a rather poor index of eutrophication of the North Sea coastal areas (Table 9).

A major factor is the sole fishery itself. Changes in the sole fishery may have had its influence on the biological characteristics of the sole stock. Table 10 gives the estimates of the fishing mortality coefficient *F* of 4, 5 and 6 year old male and female soles by years derived from Virtual Population Analysis. These age groups have been chosen because the fishery tends to concentrate on these rather than on younger or older soles. Relevant to the problem of fishing intensity is the type of gear used. In a number of countries fishermen and biologists worry about the possible ill-effects of disturbing bottom layers by active gears (ICES, 1971; 1972a; 1973c). It is claimed that the use of heavy chains attached to beam trawls may kill valuable food animals and turn rich feeding grounds into waste lands. Chains are in use in active gear such as otter trawls and beam trawls, but it is the heavy beam trawl that makes it possible to carry a large number of chains (up to 12) on one gear in twin beam trawling.

Table 8. Monthly surface water temperatures of the lightvessels "Texel" and "Vyl" combined, by years

Year	Numbers of days with surface temperatures		Average surface temperature August + September in °C
	> 14°C	> 15°C	
1957...	105	81	16·0
1958...	109	86	16·7
1959...	121	103	17·5
1960...	100	70	16·4
1961...	129	107	16·2
1962...	87	41	15·3
1963...	93	67	16·0
1964...	99	72	16·1
1965...	90	58	15·7
1966...	103	76	16·0
1967...	117	93	16·9
1968...	111	83	16·4
1969...	115	91	17·4
1970...	116	85	16·5
1971...	122	88	16·7
1972...	95	76	16·1
1973...	120	95	17·0

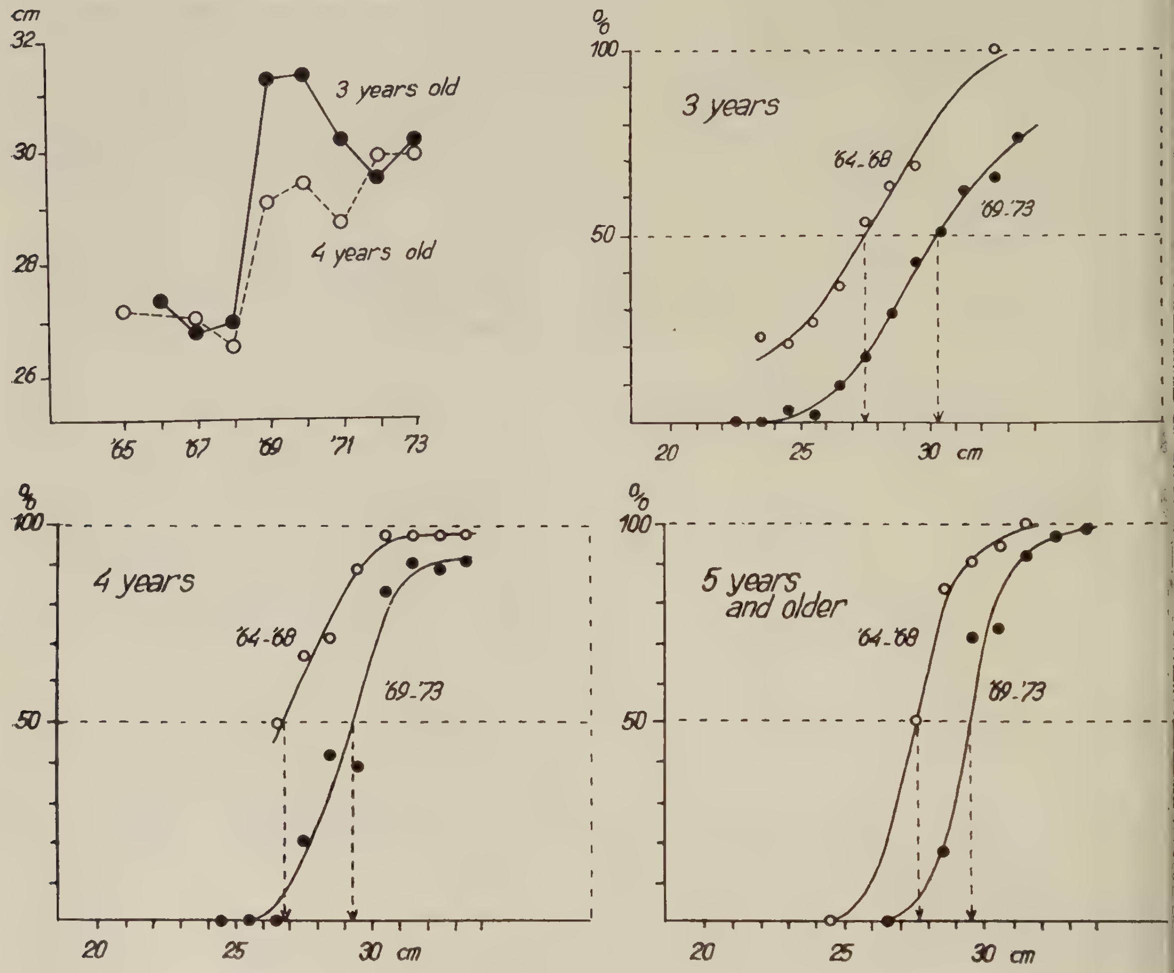

Figure 15. The 50% points of ogives of 3 year and 4 year old female soles by years; and the average ogives for 1964–68 and 1969–73 for 3 year old, 4 year old and 5 year and older soles.

The total number of fishing hours by Dutch beam trawlers (catching over 80% of all landings of sole in the North Sea) can be taken as an index of the disturbance of the bottom layer (Table 11). Not only beam trawlers disturb the bottom; the otter trawl can dig into the bottom with its chains although the effect is much less pronounced. In order to have an index for the number of "chain fishing hours" the beam trawl hours must be converted into otter trawl hours to take account of the larger amount of chains on the beam trawl.

Since 1962 the ratio between the catch-per-effort of the beam trawl to that of the otter trawl on the same fishing grounds in the Dutch sole fisheries rose from 2 to 1 to 3 to 1 in 1968. Thus the number of hours fishing by a beam trawler is now equivalent to three times the number of hours fishing by an otte trawler on the same ground.

The total hours fishing of the Dutch beam trawler can be expressed in equivalent otter trawl hours an together with the existing otter trawl hours will giv a more complete index of the impact of chains o the bottom than the beam trawl hours alone. Tabl 12 gives the totals of otter trawl hours and convert beam trawl hours of the Dutch fisheries.

For the comparison between the changes in stoc parameters described earlier with the above men tioned environmental factors only quantitative biol ogical characteristics have been used such as L_∞ W_∞, K, t_0, H and k, the condition factors q and th annual weight increments of 3–6 year-old sole sexes combined. Qualitative features remaining un

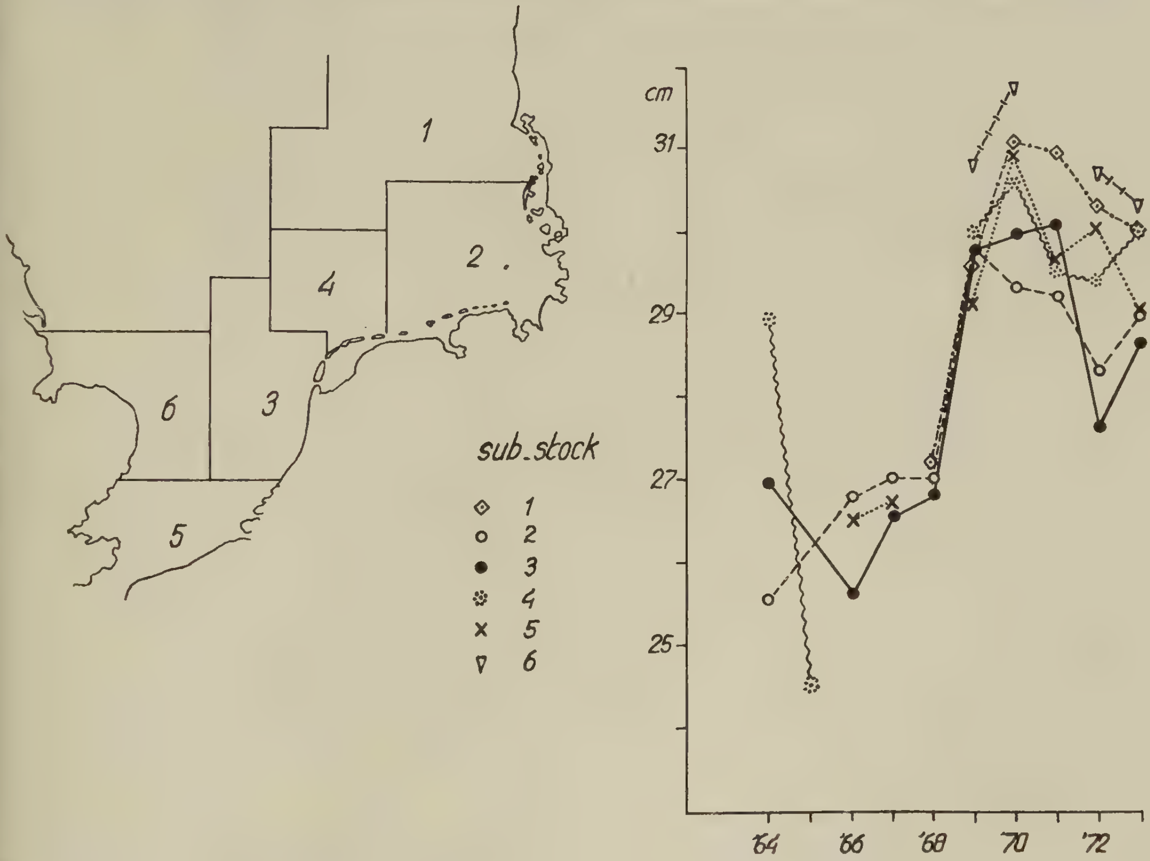

Figure 16. The 50% points of ogives for the 6 sub-stocks shown in the left hand figure.

changed (maturity-age) or showing two levels (maturity-length) were not considered in the comparison. Spearman's rank order correlation coefficients were determined for the variables summarised in Table 13 and the results of these calculations are discussed in the next section.

Discussion

In the preceding sections a number of changes have been considered. Summarized they are as follows:

1. In the period 1957–1973 *length-at-age* started to *increase* in *1963–1964* and continued to increase up to the present.
2. The annual length increments for age groups 4 and older did not change.
3. In the 0-group soles a small increase in length took place only, too small to account for the observed large increase in older soles.
4. Consequently the observed change was induced in the 2 and 3 year old soles and the factors responsible for it have to be looked for in the more inshore areas where these age groups occur.
5. In 1968–1973 length-at-age values for different sub-stocks were identical, all showing the same increase. This implies that the responsible factors are not local but involve all coastal areas.
6. *Weight-at-age* started to *increase* in *1963–1964.*

Table 9. Index of eutrophication of the Dutch coastal area: average orthophosphate content of the river Rhine, near the Dutch–German frontier in metric tons per year

Year	1957	1958	1959	1960	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971
PO_4-P	4793	4257	3879	7159	9272	6780	8042	8925	15 547	14 538	13 403	14 196	15 137	16 241	13 403

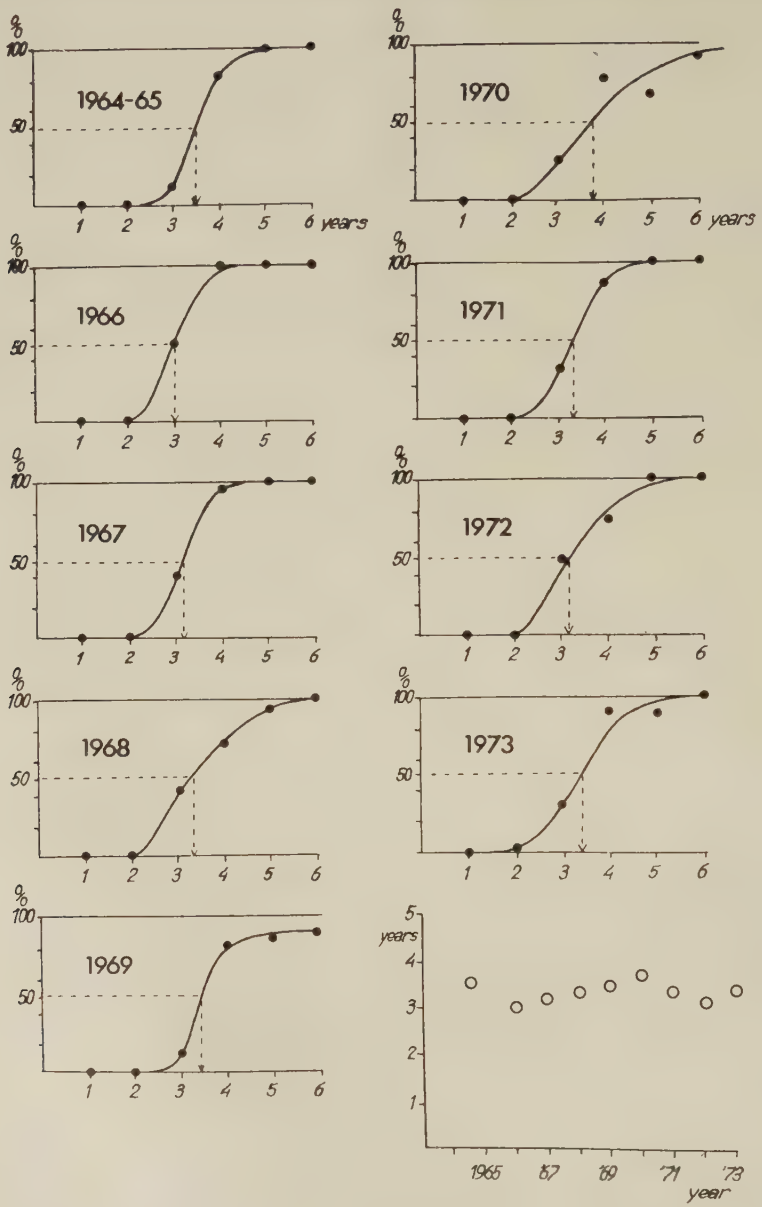

Figure 17. Maturity-ogives in May–June for female soles reaching at least stage 4, by years against age; 50% ages of these ogives.

This was caused by the increase in length-at-age and a significant *increase* in the *condition factor* which also started in *1963–1964*.

7. The relationship between *ovary weight* and *age* of female soles started to *change* in *1965*.
8. *Maturity-length* constant for a long period (1892–1968), *changed* in *1969* to a $2\frac{1}{2}$ cm higher level and has remained there since.
9. *Maturity-age*, apart from fluctuations, stayed at a constant level.
10. The Von Bertalanffy growth parameters L_∞ an W_∞ showed a significant *increase* both for male and females. The *decrease* in K and t_0 in female is doubtful and is not significant for males.
11. The coefficients of anabolism(H) and catabolis (k), derived from the original Von Bertalanff equation, as used by Nielsen (1973), showed significant *increase* since *1965–1966*.

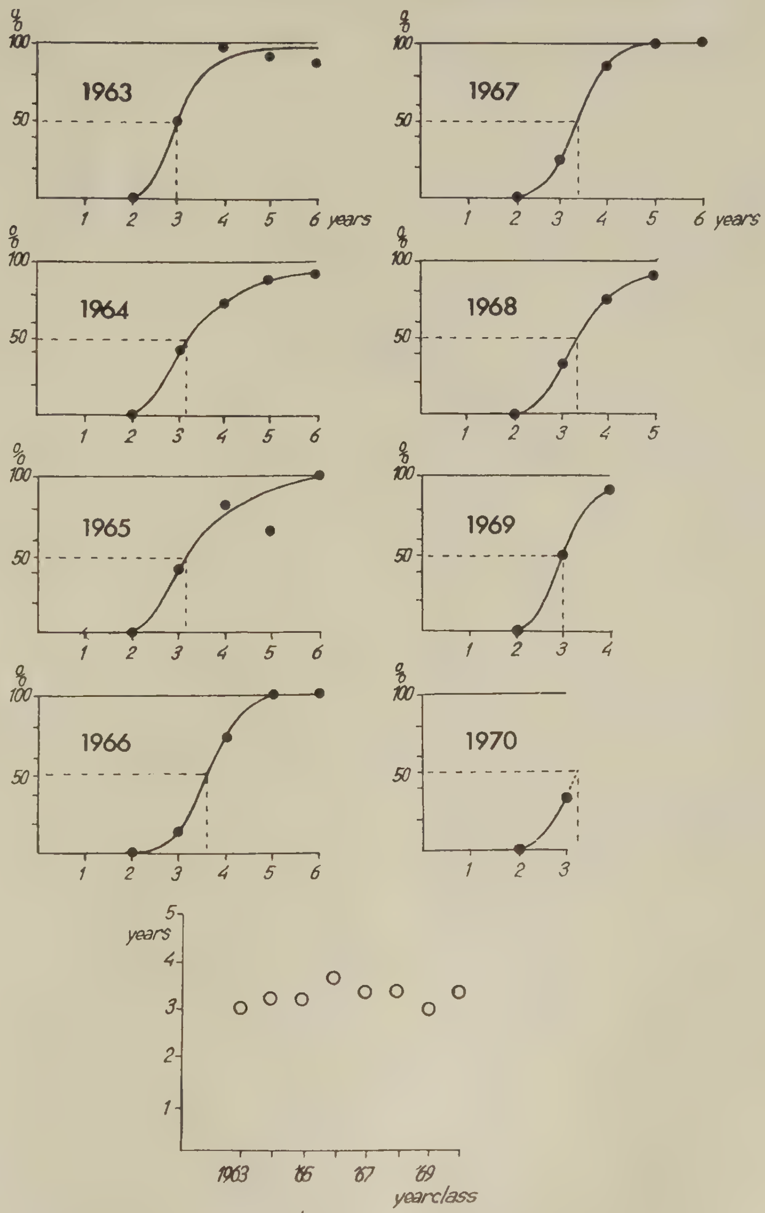

Figure 18. Maturity-ogives in May–June for female soles per year class; 50% ages of these ogives.

The results show that in general the biological parameters started to change in the years 1963–1969. However, length, weight and condition factors demonstrated this change already in 1963–1964, whereas the change in fecundity came one year later and the change in the maturity – length relationship in 1969. The reasons for these time lags is still obscure. It is possible that the increase in length and weight-at-age has to exceed a given threshold value before fecundity starts to react. The fact that in 1965 the ovary length and age relationships changed rather abruptly instead of gradually over a number of years may imply there was a fixed relationship in the pre-1963 period and that after two years increase in length and weight the sole had to change to another fixed relationship which remained constant from 1965 to 1973. In these years length and weight-at-age still continued to increase. If our conclusion

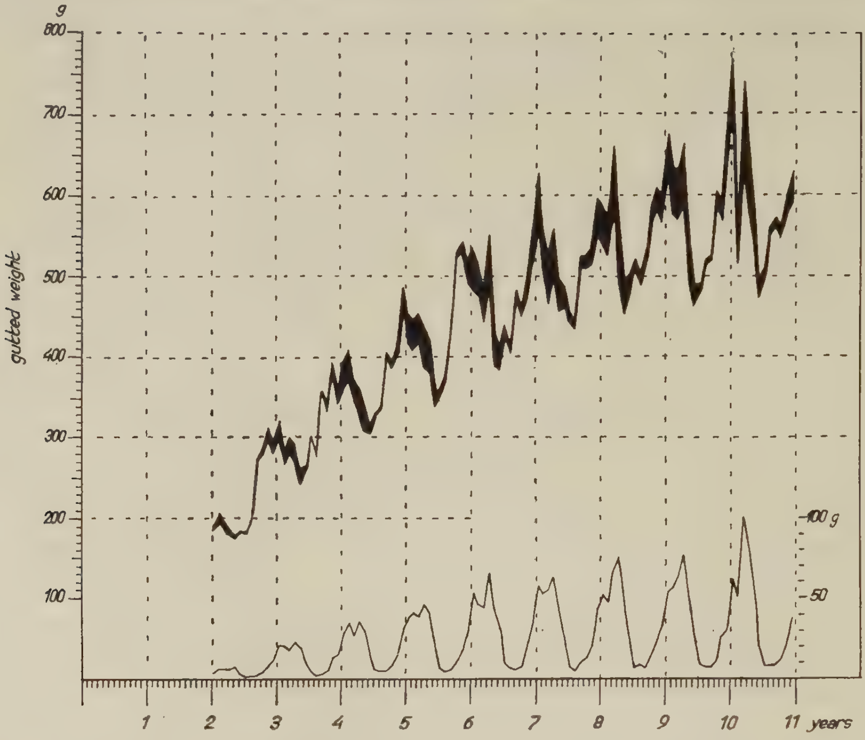

Figure 19. Average monthly gutted weight with gonads (upper curve) and female gonad weight (black) at age based on 1962–73 data. In the lower diagram gonad weight is shown separately on a larger scale.

Table 10. Estimates of the fishing mortality coefficient *F* for male and female 4–6 year old soles derived from Virtual Population Analysis. *M* = 0·10

Year	Value of *F*	
	males	females
1957	0·13	0·21
1958	0·13	0·21
1959	0·17	0·21
1960	0·19	0·27
1961	0·29	0·27
1962	0·26	0·39
1963	0·37	0·37
1964	0·34	0·43
1965	0·26	0·28
1966	0·12	0·13
1967	0·18	0·19
1968	0·37	0·42
1969	0·89	0·65
1970	0·67	0·50
1971	0·52	0·54
1972	0·72	0·55
1973	0·77	0·66

on fixed fecundity – length and – age relationship levels is correct, another abrupt change may occur in the future when length and weight continue to increase at the present rate. At the moment (1973) there is no sign of such a new change.

The same reasoning may be applied to the change in the 50% maturity length. From Figures 17 and 18 it follows that the 50% age at first maturity remained more or less constant at 3·2 years. The increase in length-at-age normally should have led to a continuous decrease in the 50% age and if no change in the 50% length had taken place, recruitment to the spawning stock would have now been at an earlier age. It may be that this is an impossible physiological change for the sole and that for some unknown reason the sole is not able to mature at an age earlier than roughly three years.

In favour of this idea is our observation that in the years 1962 to the present, soles of age group II start to develop gonads but fail to reach maturity in that year. The partially developed gonads are resorbed at the end of the spawning season (de Veen, 1970).

Possible changes in the future concerning fecundity and length at first maturity can only be considered by extrapolating on present trends when more is known about the factors responsible for the observed changes that have been discussed.

Table 11. Total number of beam-trawl-fishing hours fished by Dutch beam trawlers, $n \times 10^{-3}$.

Year	Number of beam-trawl fishing hours $\times 10^{-3}$
1957	0
1958	0
1959	0
1960	0
1961	0
1962	97
1963	152
1964	289
1965	424
1966	515
1967	1015
1968	829
1969	673
1970	723
1971	841
1972	834
1973	946

The matrix of correlation coefficients in Table 13 may help in this respect. Although significant correlations alone do not tell us anything of causal relationships, a non-significant correlation at least implies that the relevant factor can be dismissed from the list of potential factors. When looking at Table 13 it is obvious that most of the correlation coefficients are not significant. Those which are probably significant ($P < 0{\cdot}05 > 0{\cdot}01$) are given in bold types and those which are significant ($P < 0{\cdot}01$), are underlined bold types. There is no correlation between stock density in numbers and weight of the 2–15 year-old soles, and of the 2 and 3 year-old fish with the biological parameters. Nielsen (1973), using sole length-at-age data from the Danish coastal area and comparing these with stock densities in the southern and central North Sea sole failed to find any density dependent growth. A limitation of her comparison is that she could only use length-at-age data from a restricted area, namely the northern part of the area occupied by the North Sea sole. But when using length and weight data representative for the whole area there is no indication of any density-dependent mechanism as our study reveals.

In another flatfish species in the North Sea, the plaice, density-dependent growth was assumed by Beverton and Holt (1956). Hempel (1957) failed to find this mechanism in the adult plaice using empirical German data and recently the ICES North Sea Flatfish Working Group (ICES, 1972b) could only demonstrate retarded growth in the exceptionally strong year class of 1963, but not in other year classes and concluded that in general there is no evidence in plaice supporting a density-dependent mechanism in growth.

The next factor to be considered is temperature. In Table 13 no single significant correlation can be found for the relationships of temperature in the growth season and the biological parameters. This may be partly due to the fact that no representative series of bottom temperatures was available and that data of surface temperatures of two light-vessels have been used instead. For the moment we can disregard any effect of temperature on growth and fecundity.

The probably significant correlation between the index of eutrophication used and W_∞ for males may be understood as indicating an increased level of abundance of food animals. However, the rate of eutrophication, although restricted mainly to the coastal areas and thus agreeing well with the observed changes in length and weight in the 2 and 3 year old soles, is decreasing with increasing distance from the mouth of the river Rhine and does not explain why the increase in length is the same for all sole substocks. The fishing mortality coefficient of 4–6 year old soles is probably significantly correlated with W_∞ and L_∞ but not with K, t_0, H, k, and the condition factor q.

In the period under consideration changes in fishing mortality were mainly caused by changes in the Netherlands fishing effort. This changed from otter trawling with at most four to five chains to beam

Table 12. Total number of equivalent otter-trawl fishing hours fished by Dutch otter and beam trawlers, $n \times 10^{-3}$

Year	Number of equivalent otter-trawl fishing hours $\times 10^{-3}$
1957	480
1958	500
1959	550
1960	678
1961	770
1962	989
1963	1002
1964	1229
1965	1485
1966	1985
1967	3504
1968	2981
1969	2448
1970	2357
1971	2700
1972	3541
1973	3958

Table 13. A matrix of Spearman's rank correlation coefficients of the biological parameters with environmental facto
bold underlined type – significant.

		Eutrophication	Fishing effort		Fishing mortality		Temperature				Stoc
		PO_4-P in the river Rhine	Number Dutch equivalent ottertrawlhours	Number Dutch beamtrawlhours	F ♀ 4–6 years	F ♂ 4–6 years	Average Aug–Sep surface temp. Vyl, Texel	Temperature sum > 15°C	Temperature sum > 14°C	2–3 years in weight	do, in numbers
Von Bertalanffy growth parameters	W_∞ ♂	**0·72**	**0·87**	**0·82**	–	**0·64**	0·42	0·38	0·38	0·06	−0·1
	W_∞ ♀	0·56	**0·70**	**0·65**	**0·78**	–	0·39	0·29	0·28	−0·20	−0·4
	L_∞ ♂	0·33	0·48	0·48	–	**0·67**	0·12	0·05	0·10	−0·02	−0·2
	L_∞ ♀	0·60	**0·76**	**0·69**	0·72	–	0·54	0·54	0·53	0·00	−0·2
	K ♂	−0·27	−0·10	−0·03	–	−0·15	−0·40	−0·26	−0·35	−0·45	−0·3
	K ♀	0·22	−0·55	−0·49	−0·49	–	−0·17	−0·10	−0·11	0·22	0·3
	t_0 ♀	−0·23	−0·52	−0·54	−0·37	–	0·07	0·11	0·07	0·13	0·2
	H ♀	0·50	**0·74**	**0·74**	0·41	–	0·11	0·03	0·17	0·19	−0·0
	k ♀	0·25	0·61	0·61	0·24	–	0·32	0·24	0·38	0·30	0·1
Condition factor	q ♂	0·43	0·47	0·41	–	0·13	−0·11	0·06	0·08	0·35	0·3
	q ♀	0·49	**0·77**	**0·73**	0·39	–	0·06	0·20	0·25	0·14	0·0
Annual weight-increment	3–6 year old soles	**0·67**	**0·74**	**0·71**	**0·73**	**0·65**	0·29	0·24	0·29	0·03	−0·2
	trend eliminated	−0·24	−0·29	−0·29	−0·02	−0·21	0·14	0·22	0·33	0·12	0·1
Stock density	2–15 year numbers	0·06	−0·24	−0·20	**−0·70**	−0·57	−0·17	−0·13	−0·10	–	0·3
	2–15 year weight	0·39	0·18	0·20	−0·20	−0·03	0·00	0·00	0·06	0·04	
	2 + 3 year numbers	0·06	−0·28	−0·26	−0·56	−0·54	0·14	−0·06	0·01	**0·90**	
	2 + 3 year weight	0·35	0·03	0·06	−0·36	−0·29	0·19	−0·08	0·02		
Temperature	Sum > 14°C	−0·06	0·06	0·04	0·26	0·22	**0·76**	0·61			
	Sum > 15°C	−0·10	0·02	−0·01	0·24	0·19	**0·80**				
	Average temp. Aug–Sep	0·17	0·05	0·03	0·29	0·33					
Fishing mortality	F ♂ 4–6 years	0·52	0·63	0·55	**0·96**						
	F ♀ 4–6 years	0·43	0·57	0·49							
Fishing effort	Number Dutch beam trawl hours	**0·78**	**0·98**								
	Number Dutch equivalent otter trawl hours	**0·76**									
PO_4-P in river Rhine											

trawling with more than ten chains. Thus the number of Dutch beam trawl fishing hours is not only an indication of this increased fishing effort but of the effect of chains on the bottom layers as well. A still better index of this effect is the equivalent otter trawl hours.

The significant correlation coefficients for both the beam trawl fishing hours and the equivalent otter trawl hours with W_∞ for both sexes and probably significant for L_∞ and H and the female condition factor, implies that we may have traced a significant factor.

When plotting the condition factor values against equivalent otter trawl hours (see Fig. 21) a close relationship seems to exist in the females but less so in the males. Still this does not tell us much, the more so because the correlation is based on variables in two time series.

Additional evidence should be collected before we may identify causal relationships. In the case of the condition factor the curves in Figure 21 show an intercept on the Y-axis of 0·0076–0·0078. This could be the situation in an area without any influence of chains on the bottom layers. El-Zarka (1963), reporting on Mediterranean soles near Egypt and on soles transplanted from the Nile delta to Lake Quarun gives length and weight-at-age data sampled throughout the year. The average annual condition factor for these soles was 0·0085 for the Mediterranean and 0·0082 for the Lake Quarun soles.

uch as stock density, temperature, fishing mortality, fishing effort and eutrophication. Bold type -- probably significant,

ensity		Annual weight increment		Condition factor		Von Bertalanffy growth parameters								
2–15 years in weight	do, in numbers	Trend eliminated	3–6 years old soles	*q* ♀	*q* ♂	*k* ♀	*H* ♀	*t₀* ♀	*K* ♀	*K* ♂	*L*∞ ♀	*L*∞ ♂	*W*∞ ♀	*W*∞ ♂
0·12	−0·31	−0·14	**0·79**	–	0·52	–	–	–	–	−0·22	–	0·47	–	
−0·14	−0·61	−0·01	**0·74**	0·60	–	0·36	0·50	−0·49	**−0·69**	–	**0·84**	–		
−0·44	**−0·79**	0·16	**0·67**	–	0·34	–	–	–	–	0·27	–			
0·05	−0·39	−0·03	**0·79**	**0·69**	–	0·56	0·56	−0·31	−0·56	–				
−0·35	−0·32	−0·07	−0·16	–	−0·13	–	–	–	–					
−0·09	0·33	0·43	−0·27	−0·44	–	−0·49	−0·51	**0·87**						
−0·03	0·31	0·47	−0·21	−0·40	–	−0·51	−0·56							
0·21	−0·17	0·06	**0·70**	0·63	–	**0·86**								
0·16	−0·09	−0·04	0·52	0·58	–									
−0·27	−0·29	0·28	0·54	**0·81**										
–	–	−0·53	0·60											
−0·14	−0·55	0·31												
−0·40	−0·27													
0·79														

To make these values comparable to those for the North Sea we have to apply a factor for gutting. Using the factor of 1·125, common in use for the European sole, gives the values of 0·0076 and 0·0073 for "gutted" Egyptian soles. These values agree well with the values at the intercept in Figure 21. However, the Egyptian data were collected before 1963 and the North Sea sole condition factors of 1957–1963 were at about the same levels. Thus this example cannot be used as evidence for a causal influence of bottom disturbance and growth-rate changes.

The changes in growth were mainly imposed in the 2 and 3 year old soles occupying the coastal areas. When considering the local distribution of the Dutch beam trawl effort (Fig. 22) it is obvious that effort is maximal in the coastal areas and that from 1963–1965 to 1971–1973 there was an overall increase in this effort. Contrary to the effect of eutrophication which decrease with increasing distance from the mouth of the Rhine the average number of beam trawl fishing hours is more or less the same in all continental coastal areas fished by the Dutch at present.

Other evidence in support of a causal relationship is the observation that dabs concentrate in the path of a trawl, apparently looking for injured or excavated food animals (Margetts and Bridger, 1971). Bannister and Lee (personal communication) have observed the occurrence of the gonads of *Echinocardium* in the stomach contents of the dab in the North Sea,

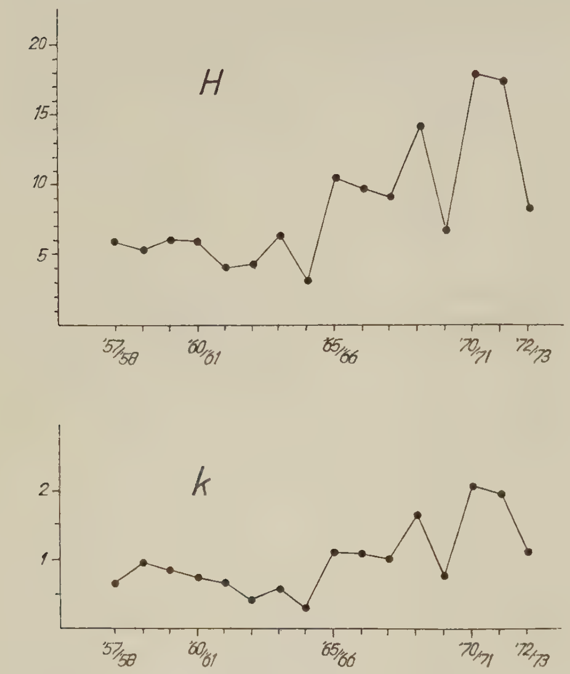

Figure 20. The coefficients of rate of anabolism H and of the rate of catabolism k for female sole by years.

an unlikely occurrence if the *Echinocardium* had not already been damaged by gear. Arntz and Weber (1970) have discussed the importance of *Cyprina islandica* L. as food animal for cod and flounder in Kiel Bay and considered the damaging of buried *Cyprina* by the digging action of trawl doors as a possible explanation of the increased quantities in the stomach of both species. Daan (1973) assumes that the same is true for the North Sea, where *Cyprina* is tossed about first and partly broken up before being an easy food supply for cod.

Up to the present there is no direct evidence of an increased availability of molluscs and polychaetes for sole. De Groot and Apeldoorn (1971) have studied the damage to beam trawl caught zoobenthos and demonstrated heavy damage to most bottom organisms. The sole is not an active feeder and has to rely on its chemical receptors for locating food. Under normal conditions it has to spend a certain amount of energy to find and dig out its prey. In a situation where beam trawl chains have damaged bottom animals, location of food might be made easier by stronger olfactory stimuli from the injured zoobenthos and less digging is needed. Thus, hypothetically, less energy would then go into searching for food and more could be transformed into growth.

To prove that this is a correct assumption needs further research, mainly through controlled experiments. However, there is a good chance that the answer will be given in a few years. The regulation by NEAFC of the demersal fisheries in the North Sea by setting Total Allowable Catches for 1975 and 1976 implies a substantial decrease in the fishing effort and provided this reduction is effectively realised the influence of beam-trawling with chains will diminish. The values of the biological parameters in the coming years will no doubt tell us if our assumptions are right or wrong.

Summary

In the period from 1957 to the present market sampling has made it possible to follow biological parameters in the North Sea sole stock continuously. Changes in a number of these parameters have taken place together with changes in the fishing effort. The sole stock was in a situation of under-exploitation in 1957 which remained to 1963, then passed the point of optimum exploitation quickly in 1964–1965 and entered increasing overfishing in 1966 which led to the present serious problems.

In the various sole sub-stocks in the North Sea an increase in growth took place, at first slowly but more

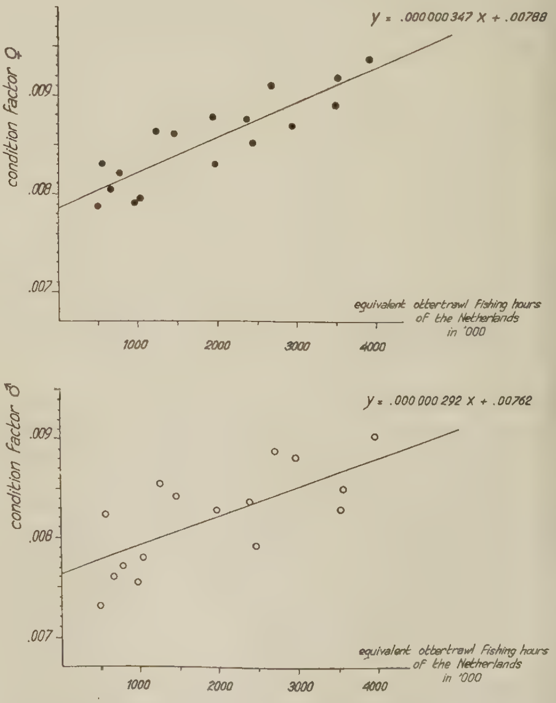

Figure 21. The relationship between condition factor for males and females and the index of disturbance of the seabed by heavy chains in the Dutch beam trawl fisheries.

rapidly since 1963–1964. Length and weight-at-age together with the condition factor continued to increase regularly, as did the weight of the ovary.

The 50% length at first maturity, for a very long period constant, changed to a 2·5 cm higher level in 1969 and remained at that level since. The 50% age at first maturity did not change.

The relationship between ovary-weight per year group and age changed in 1965 to another form of relation which remained constant since that year.

The Von Bertalanffy growth parameters L_∞ and W_∞ increased in both sexes, K and t_0 probably decreased in females but remained constant in males. Both the coefficients of anabolism and catabolism changed in females.

No correlation could be demonstrated between the biological parameters and stock size in numbers or weight. The same was true for water temperatures in the growth season.

For W_∞ in males only there was a correlation with the index of eutrophication used – the amount of orthophosphate in the river Rhine.

A significant correlation was found for condition factors, L_∞ for females, W_∞ for both sexes, and the coefficient of anabolism for females with the number of beam trawl fishing hours and with the index of bottom disturbance – the number of equivalent otter trawl fishing hours. Additional evidence on distribution of fishing effort by beam trawlers points to the possibility that the amount of bottom disturbance by heavy chained beam trawls may have a positive effect on growth in soles. Food organisms are injured by the gear and made more easily available for soles, which may economize on energy for searching, locating and digging out food and may thus transform more energy into growth.

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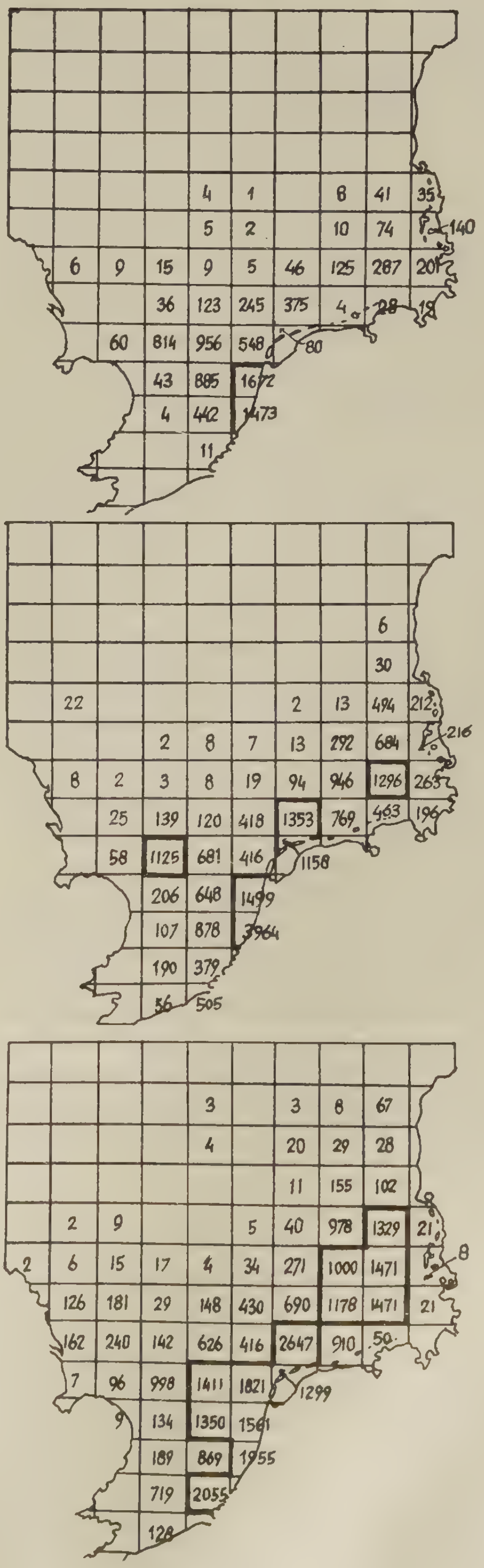
4 1 8 41 35
5 2 10 74 140
6 9 15 9 5 46 125 287 201
36 123 245 375 4 28 18
60 814 956 548 80
43 885 1672
4 442 1473
11
6
30
22 2 13 494 212
2 8 7 13 292 684 216
8 2 3 8 19 94 946 1296 265
25 139 120 418 1353 769 463 196
58 1125 681 416 1158
206 648 1499
107 878 3964
190 379
56 505
3 3 8 67
4 20 29 28
11 155 102
2 9 5 40 978 1329 21
2 6 15 17 4 34 271 1000 1471 8
126 181 29 148 430 690 1178 1471 21
162 240 142 626 416 2647 910 50
7 96 998 1411 1821 1299
9 134 1350 1561
189 869 1955
719 2055
128

Figure 22. Average numbers of hours fishing by Dutch beam trawlers in the growth season of the sole (3rd quarter) by rectangles for the periods 1963–65 (top), 1967–69 (centre) and 1971–73 (bottom). Rectangles where fishing effort exceeded 1000 h are indicated.

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A proposed aerial/acoustic strategy for pelagic fish stock assessment

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Aerial and acoustic observations on *Sardinops ocellata* shoals in the Southeast Atlantic show that the extreme patchiness of the shoals, the mobility of the fish and their tendency to avoid vessels, may invalidate the results of quantitative acoustic surveys on the stock. It is suggested that these survey errors can be reduced considerably by employing an aerial/acoustic strategy where the aircraft locates and measures the shoal area, and the vessel makes synchronous measurements of shoal thickness and packing density from as many shoals as possible. The combined data provide a direct estimate of stock size.

Introduction

In mid-1970 it became apparent that serious depletion had occurred in the commercially important stock of the Southeast Atlantic pilchard, *Sardinops ocellata* Pappé. Accordingly, the Sea Fisheries Branch of the Department of Industries launched a large multi-disciplinary research programme to determine the extent of the decline and to suggest appropriate management action (Cram and Visser, 1972). Since it was believed that population dynamics and catch statistics alone would not give sufficient up-to-date information to regulate a stock susceptible to rapid fluctuations, aerial and acoustic methods of measuring the stock size directly were introduced. The aerial method involves locating and measuring, at night, bioluminescent areas known to be caused by fish shoals near the surface (Cram, 1972; 1974). These observations are supplemented by synchronous measurements of shoal thickness made with standard fishing echo-sounders. A 120 kHz scientific echo-sounder and integrator with towed transducers has been used to determine the fish density within the shoals. Recently the integrator has been replaced by a digital data-logging system (Hampton and Claum, 1975).

Initially it was intended to determine the horizontal distribution and area of the fish by independent aerial and acoustic techniques, so that the two methods would provide a check on one another. However, experience of pilchard distributions and shoal behaviour, gained mainly from aerial observations, have shown that independent acoustic determinations of shoal horizontal dimensions are susceptible to three survey errors which may be sufficiently severe to invalidate the results. These are:

1. the extreme patchiness of the shoals over the population's range;
2. the mobility of the fish;
3. the tendency of the shoals to avoid survey vessels.

These factors could invalidate results obtained from independent acoustic surveys upon any fish with shoaling behaviour similar to *S. ocellata*.

Due to the above survey problems and the fact that biological conditions in the survey area favour aerial observations, independent acoustic surveys have been abandoned in favour of a combined technique where the horizontal dimensions are determined from the air, and shoal thickness and fish density are measured synchronously by the scientific sounder and data-logging system.

Acoustic determination of shoal horizontal dimensions

Patchiness

In the coastal upwelling zone of the Southeast Atlantic, pilchard shoals are normally found grouped in a number of relatively large discrete areas varying considerably in size and distributed over the area in a generally unpredictable manner (Fig. 1). The shoal groups consist of aggregations of individual shoals (Fig. 2) in varying degrees of association with one another (Fig. 3). In making acoustic

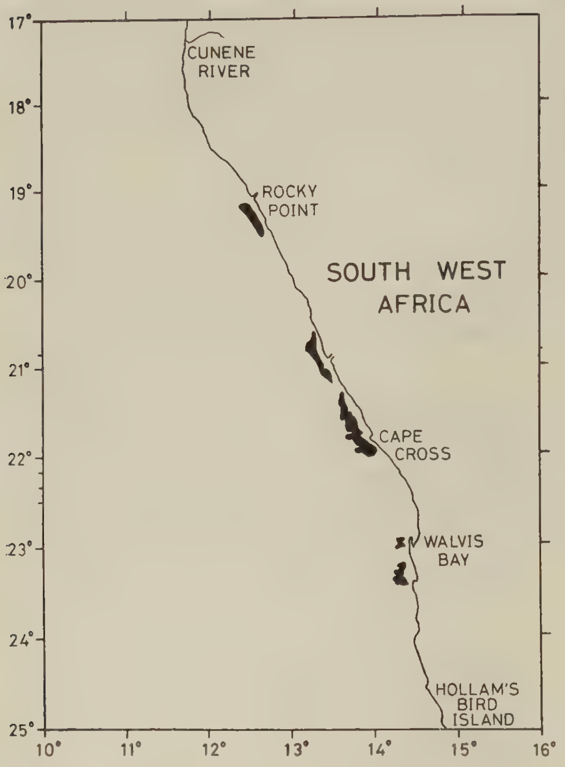


Figure 1. Pilchard shoal groups mapped by aerial survey, 3 to 12 December 1972.

stock estimates on patchy distributions of this kind, the approach commonly used for demersal fish, where the stock size is estimated from interpolations of abundance measurements along regular survey lines covering a widespread area (for example Cushing, 1968), will not necessarily be valid, as this method applies best to fish sparsely and continuously distributed over the survey area.

To examine this point quantitatively, we have simulated a number of such acoustic surveys on the pilchard distribution shown in Figure 1 and obtained the variance in the abundance estimates expected from each of the simulated surveys. A series of imaginary, but typical grids was superimposed on Figure 1 and fish abundance for each grid calculated from the intersection of the grid lines with detailed maps of the individual shoal groups contoured in categories of horizontal density (e.g. Fig. 3). It was assumed that on a transect across a contoured area a survey vessel would encounter fish over a fraction of the transect equal to the fractional cover of fish within the area. It is appreciated that this assumption may not be valid, particularly in areas of lower fractional cover, and that it would be more correct to use smaller scale maps showing the individual shoals. However, the shoals were too numerous to measure individually with the aerial technique employed at the time, so the above assumption was adopted, accepting that the variances would be underestimates reflecting only part of the sampling error.

The simulated surveys consisted of 4 series of rectangular grids chosen to cover the area from 17°00′S to 25°00′S on E/W lines 45 n m long and spaced 40, 30, 20 and 10 n m apart respectively. This covers the area of known pilchard occurrence. The ship's survey speed was taken as 5 knots which is our usual speed when towing transducers. (Although vessels employing hull-mounted transducers will travel faster than this, we have chosen to limit the simulation to our own conditions). At 5 knots the surveys would take approximately 8·5, 10, 13, and 22 days respectively to complete which covers a range of typical acoustic survey durations. Each series consisted of 10 grids, each displaced 0·1 of a line spacing to the south of the previous grid in the series. The displacements between successive grids in the 4 series were therefore 4·0, 3·0, 2·0 and 1·0 n m respectively.

The results of the simulation are shown in Table I. $\bar{A}$ is the mean area of the fish calculated from the 10 grids in the series and σ the corresponding standard deviation. ΔA is the difference between $\bar{A}$ and the area estimated from the actual aerial survey by measuring the contoured areas in Figure 3 and similar contour maps of the other shoal groups. This area was found to be 109 n m^2.

It will be noted that the means lie close to the aerial value and that as expected, ΔA decreases with survey length. The values of σ do not show as clear a trend, probably because 10 grids are insufficient to give a quantitative relationship between standard deviation and survey duration.

Table 1. Summary of simulated acoustic survey results. For further explanation see text.

Series No.	Line spacing (nm)	Grid duration (days)	$\bar{A}$	σ	ΔA
			(n.miles^2)		
1	40	8·5	95	26	−1
2	30	10	117	43	
3	20	13	105	39	−
4	10	22	109	24	

In order to determine whether the errors possible from a single acoustic survey would be acceptable for a stock estimate to regulate the fishery, we have taken as an example the decline of the Cape pilchard

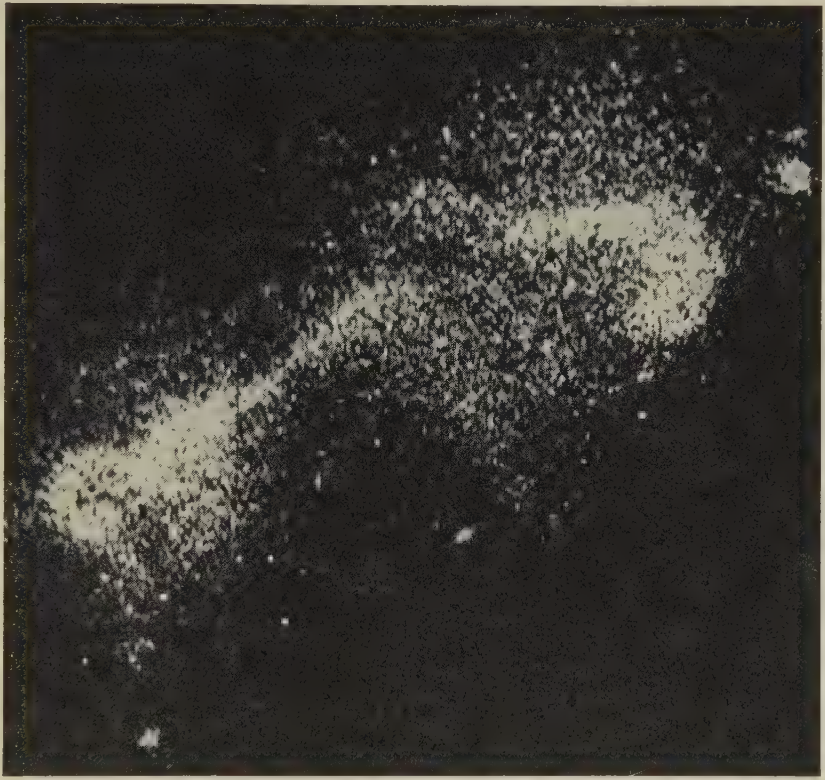


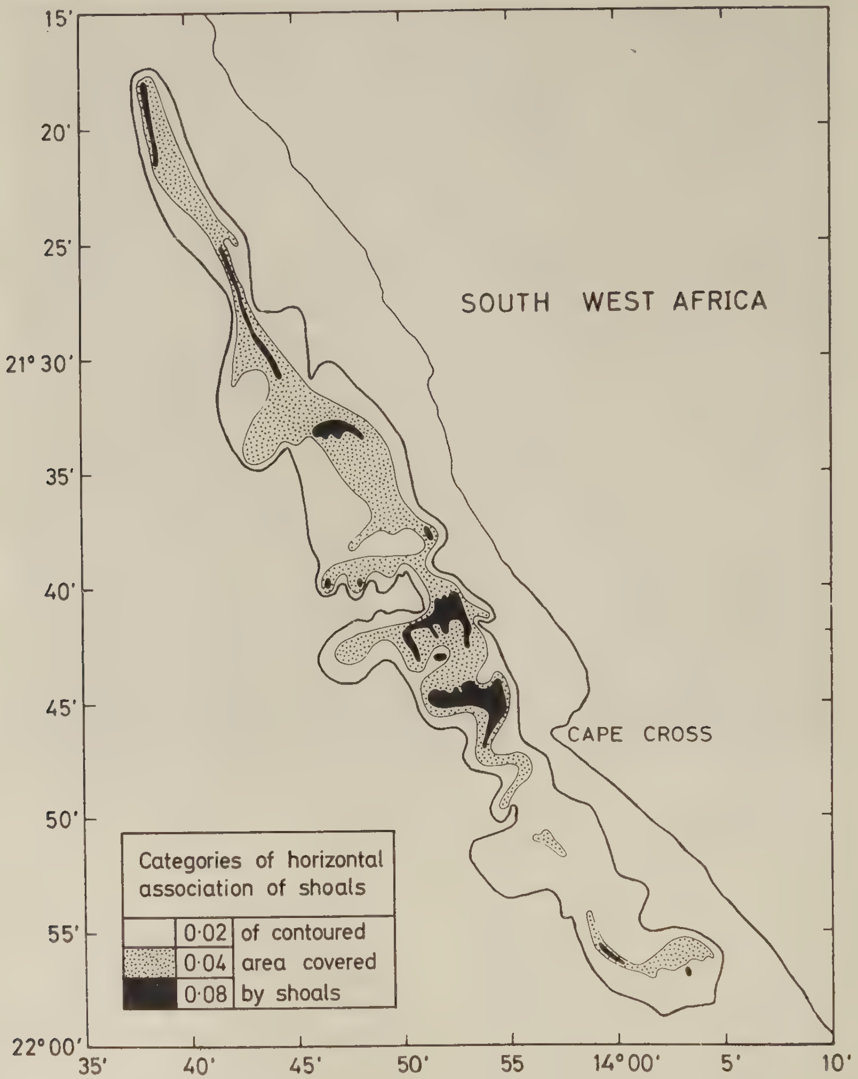
Figure 2. Two individual pilchard shoals detected by low-light-level television camera. Photographed off videotape. Shoals approximately 500 m and 900 m long respectively.

S. *ocellata*) stock between 1963 and 1966. Between hese years the catch declined at an average rate of 5% per annum after being stable for three years Stander and Le Roux, 1968; Baird, in press), and ssuming that this was the rate of decline of the tock, a stock assessment technique sensitive to an- ual changes of say 25%, would have been necessary o decide that remedial action was necessary. Of the 0 simulated grids, 19 (47%) gave areas differing y more than 25% from the aerial value. These iscrepancies represent errors in determining the rea of the fish in Figure 1 from a discrete number of ransects, and provided that the distribution is typical, he discrepancies are valid measures of the survey rrors to be expected regardless of errors in the aerial stimate of shoal area used in the simulation.

The sampling errors demonstrated by this simple imulation are significant even though they represent nly part of the overall sampling error. Although he simulation is of an acoustic survey on one known istribution only, it serves to demonstrate semi- uantitatively the sampling errors likely to arise rom the patchy distribution of the fish.

Shoal mobility

A number of observations extracted from previously collected aerial data have shown that pilchard shoal groups may move considerable distances in the time required to complete an acoustic survey with towed transducers. One such case is illustrated in Figure 4 where a shoal group was observed to move 27 n m southward in 24 h, averaging approximately 1 knot. A vessel surveying this area on 45 mile long lines, 10 miles apart as in series 4 of the simulation, would also progress southwards at approximately 1 knot, and measurements of shoal horizontal extent would be meaningless. Even on the coarsest grid the speed southward would only be 2·3 knots and the north/south extent of the shoal would be overestimated by more than 40%. Errors of the same order would be introduced on northwards surveys. Although ship-board sightings, sonar, and a knowledge of general migratory patterns can give some indication of the general direction of shoal movement, this information is inadequate for any form of quantitative correction and only indicates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SOUTH WEST AFRICA
CAPE CROSS
Categories of horizontal association of shoals
0·02 of contoured
0·04 area covered
0·08 by shoals

Figure 3. Distribution of individual shoals within largest shoal group in Figure 1. Map made from aerial survey, 5 December 1972.

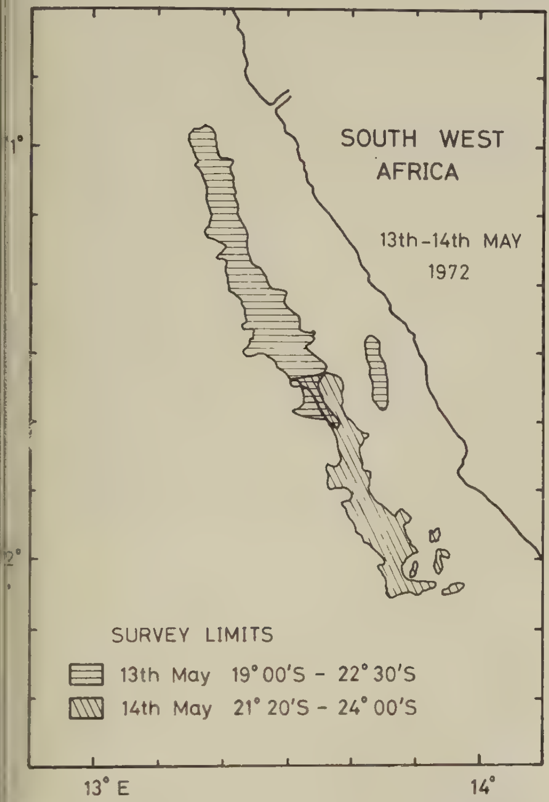
whether measurements would be positively or negatively biased.

Shoal movement therefore constitutes a source of serious error which increases with duration of survey, so that the advantages of mounting longer surveys to reduce the statistical sampling errors described in the previous section are largely offset.

Shoal avoidance

From the air we have frequently observed pilchard shoals avoiding an approaching vessel by splitting in its path or turning to one side. Although we have no photographic evidence to prove that shoals ha avoided survey vessels entirely, comparisons betwee echo-sounder recordings from a hull-mounted tran ducer and a transducer towed 130 m astern at t same time, have demonstrated that the towed tran ducer missed many shoals lying in the ship's trac During a survey from 16 to 18 May 1973, it w found that while 68 shoals were detected by the hul mounted transducer, only 13 shoals and a few fra ments were detected by the towed transducer.

Even more severe difficulty has been experience in detecting pilchard shoals near the surface with upward-sounding 120 kHz transducer towed at 15



igure 4. Southward movement of a shoal group in 24 h etween 13 and 14 May 1972. Shoals mapped from aerial urvey.

epth. Shoals have often not been detected even hen known to be present from aerial and shipoard sightings, and it is concluded that shallow hoals in the path of the transducer are usually diturbed by the towing cable which must pass through he fish before the shoal is insonified.

These observations indicate that under our condiions, measurements of shoal horizontal cover obained from towed transducers are not quantitative. lthough shoal avoidance could probably be reduced y towing more slowly, both the statistical sampling rrors and the problems due to shoal movement ould be aggravated, and the overall accuracy would ot necessarily be improved. Avoidance errors apear smaller if the hull transducer is used, but it is till not known whether the errors fall within acceptble limits.

Aerial shoal mapping

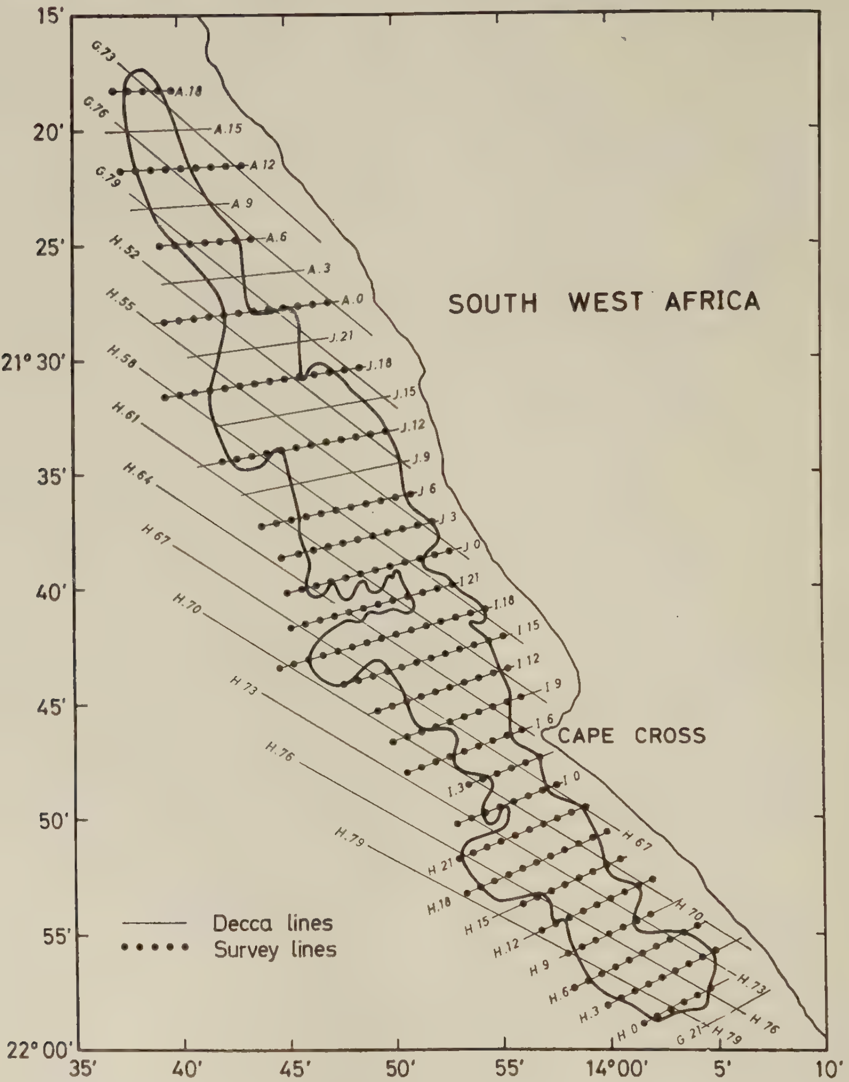
he above arguments show that it is preferable to emove from the vessel the responsibility for meauring the horizontal dimensions and distribution of the fish shoals. Fortunately this information can readily be obtained from aerial surveys. The technique has been briefly described (Cram, 1972; 1974), but for convenience the relevant parts are summarised here.

Initially, the entire survey area is surveyed sufficiently intensely to locate and delineate all shoal groups. Close surveys are then mounted on each shoal group in turn as follows. The bioluminescent outline of the shoal is roughly determined again, and a survey grid which will provide maximum coverage of the shoal group in the remaining dark moon period of the night, is drawn up in the aircraft. For convenience each swathe follows a Decca lane along which the aircraft's track is plotted on small scale Decca lattice charts (Fig. 5). On each swathe the bioluminescence is observed with a direct viewer, image-intensifier, or recently, a low-light-level television camera, and the fraction of the field-of-view covered by fish estimated each second. These observations are averaged to give the fraction of the swathe covered by fish, which together with a knowledge of the swathe width and length gives the area of fish shoals within the swathe. The area of fish within the whole shoal group is obtained by proportion from the sum over all swathes and the total area of fish by summing over all shoal groups.

The shoal groups shown in Figure 1 were surveyed in 10 nights of which 2 were lost due to poor weather. The close surveys on the shoal groups were considerably more intensive than possible with a survey vessel. For example, the large shoal group shown in Figure 6 was surveyed on 25 east/west lines on average 4·1 miles long and 1·8 miles apart. Total survey time was less than 3 h. At the survey altitude of 500 m the swathe was approximately 550 m wide so that 17% of the area of the shoal group was actually observed. In contrast, a survey vessel equipped with an echo sounder of 20° beamwidth steaming the same grid at 5 knots would complete the grid in 35 h while insonifying only 0·8% of the area at a depth of 10 m.

Statistical sampling errors are therefore greatly reduced by using an aircraft. In addition, errors due to shoal movement are almost negligible due to the relatively fast survey speed, and shoal avoidance problems are eliminated entirely.

All shoals must however be visible from the air if the aerial observations are to provide valid abundance estimates. We believe that this is not a serious objection in our circumstances, as echo recordings of 3931 pilchard shoals off the west coast of Southern Africa showed that at night fewer than 7% of the shoals were deeper than 8 m, which has been found to be the approximate limit of visibility under normal conditions. Shoals at depths of between 15 and 20 m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SOUTH WEST AFRICA
CAPE CROSS
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A.15
A 12
A 9
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J.9
J 6
J 3
J 0
I 21
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I 12
I 9
I 6
I 3
I 0
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H.67
H.70
H 73
H.76
H.79
H 21
H.18
H 15
H.12
H 9
H 6
H 3
H 0
G 21
H 67
H 70
H 73
H 76
H 79
Decca lines
Survey lines

Figure 5. Grid employed in aerial survey of shoal group in Figure 3.

have been observed from the air on occasion. Furthermore, low-light-level television techniques now being introduced will allow the fish to be detected at greater depths than possible with the direct viewer.

Proposed combined aerial/acoustic survey strategy

The basis of the combined method is to use an aircraft to locate and roughly map the shoal groups within the population's range, whereafter the vessel would operate synchronously with the aircraft to study each shoal group in turn. All areas between shoal groups would be ignored, thus concentratir effort into areas of known fish occurrence.

Using a low-light-level television camera with wic angle lens and videotape storage system now beir introduced, the aircraft could cover a shoal grou completely, allowing every component shoal to l located and measured in area. While these measur ments were being made, the vessel would work loose grid structured to sample shoal thickness ar target strength as widely as possible throughout tl shoal group in the time available for synchronoı study. As it would be most important to sample tl maximum number of shoals to obtain the best po sible statistical sample, the vessel would use sonar ocate the shoals and deviate from its grid whenever necessary to encounter them: the rigid adherence to a grid would not be necessary.

A purse seine vessel would work in close conjunction with the survey vessel to sample length distribution within the shoal group. This would enable the mean density (number of fish-per-unit-volume) of the shoals to be calculated from calibration data on the relationship between the length and target trength of individual specimens.

The aerial measurements of the total area of the hoals within the group, and acoustic samples of mean shoal thickness and density, will allow the otal number of fish within the shoal group to be alculated, from which the total weight of the shoal roup would be calculated from the size distribution of the fish. The size of the stock would then be stimated by summing the tonnages of the shoal roups.

Conclusion

t is concluded that the proposed aerial/acoustic echnique would be effective in reducing all three najor sources of survey error associated with independent acoustic estimations of *S. ocellata* stock ize from a single vessel. The method should be onsidered for making direct assessments on other elagic species whose behaviour and distribution atterns present survey problems similar to those ncountered with *S. ocellata*. The aerial technique hould be feasible in other pelagic fisheries (Cram, 974), and as there are no major technical difficulties n synchronising aerial and ship-borne surveys in areas erved by normal navigation systems, the combined nethod could also probably be widely applied, particularly in areas where acoustic stock estimation rogrammes have already been established. The cost of hiring an aircraft for regular surveys should be measured against the quality of the results obtainable and the more effective use of ship's time.

Acknowledgements

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Population studies of the whiting *Merlangius merlangus* (L.) of the northern North Sea

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The possibility of the existence of more than one stock within this area is considered. The data are derived from (1) conventional tagging experiments carried out along the east coast of Scotland and around the Orkneys and Shetlands from 1964 to 1972, and (2) a biological tag project using a larval cestode *Gilquinia squali*, parasitic in the eyes of whiting, conducted over the same period.

No tagged whiting were recaptured south of the Dogger Bank, thus supporting the results of earlier studies which suggested that whiting to the north and south of the Dogger Bank mix very little. Neither were any recaptured to the north or west of the Scottish mainland. Generally speaking, whiting tagged in coastal areas were recaptured within 30 miles of the coast, whereas those tagged at the Shetlands were recaptured over a wide area of the open North Sea. Whiting tagged at the Shetlands also yielded evidence of a southerly migration in summer followed by a return northerly migration in spring. The parasitological results showed a coastal strip of consistently low incidence of infection (< 5%) and an offshore area of higher incidence (usually > 10%). Around the Shetlands the incidence of infection varied from the typical offshore level in young whiting (2+, 3+) to that of the coastal area in older fish.

Both sources of information suggest that there is little interchange of whiting between coastal and offshore waters in the southern part of the study area (from the Moray Firth to the Northumberland coast), but the parasitological results suggest that some three-years-old and older whiting migrate from the Moray Firth to Shetland waters and thence to the deeper waters to the east.

Introduction

The whiting is exploited throughout the North Sea and on the grounds to the west of the British Isles, within the 200 m depth contour. The species has considerable economic importance, landings by all European nations averaging 206000 metric tons per annum during the period 1967 to 1973. The major component of these landings (on average 67% of the total) came from the North Sea. To carry out stock assessments and predict the effects of fishing on the whiting resource, it is necessary to know if the population in the North Sea is made up of a number of separate stocks that must be assessed individually.

There is already considerable evidence to suggest that North Sea whiting are divided into two separate groups distributed to the north and south of the Dogger Bank respectively. This conclusion was reached by Kabata (1967), on the basis of the frequency of occurrence of two species of protozoan parasites found in the gall bladders of whiting, and by Gamble (1959) who studied the numbers of vertebrae of whiting from north and south of the Dogger Bank. Supporting evidence also came from the tagging experiments of Rout (1962), and Williams and Prime (196
in the southern North Sea.

This paper presents results of tagging and parasi
infestation studies to determine if the group to t
north of the Dogger Bank is further divided into tw
or more stocks.

Tagging experiments 1964–1972

Methods

The whiting tagged in these experiments were caug
using conventional fishing gear (trawl, Danish sei
hand-line) either by research vessels or commerc
vessels. Most of the experiments were on fishi
grounds within 25 miles of the coast and in dep
of 100 m or less. The fish tagged were in almost ev
case greater than 25 cm in total length, two or m
years old, and had reached sexual maturity. T
types of tag were used: most fish were tagged wit
yellow or orange "flag", 40 mm × 10 mm, attac
by a braided nylon thread, but a "spaghetti" t
a yellow plastic tube with an outside diameter
approximately 1 mm, was used on several occasi

Year	Month	Area	Method of capture	Number released	Tag type	Total number returned*	%	Number with reliable data, > 28 days' absence	%
1964	Mar	Moray Firth	RV Trawl	41	Flag	6	14·6	2	4·9
	Apr	North Coast	RV Trawl						
	Apr	West Shetland	Commercial Seine	211	Flag	9	4·3	6	2·8
	Apr	East Shetland	Commercial Seine	120	Flag	2	1·7	1	0·9
	Jun	North Coast	RV Trawl	19	Spaghetti	2	10·5	1	5·3
	Aug	Aberdeen	Hand line	37	Spaghetti	4	10·8	3	8·1
	Aug	Central and Northern North Sea	RV Trawl	830	Spaghetti	16	1·9	12	1·4
1965	Apr	West Shetland	Commercial Seine	114	Flag 63 4 Spaghetti 51 1	5	4·4	3	2·6
	May	Moray Firth	RV Trawl	25	Spaghetti	1	4·0	1	4·0
	Jul	East Coast	Commercial Seine	5	Spaghetti	0	0·0	0	0·0
	Jul	Bell Rock	Commercial Seine	663	Flag 332 23 Spaghetti 331 26	49	7·4	35	5·3
	Jul	East Shetland	Commercial Seine	229	Flag	19	8·3	9	3·9
	Aug	Aberdeen	Hand Line	139	Flag	20	14·4	16	11·5
	Aug	East Coast	RV Trawl	776	Flag 526 20 Spaghetti 250 3	23	3·0	15	1·9
	Nov/Dec	Moray Firth Firth of Forth	RV Trawl	79	Flag 37 5 Spaghetti 42 4	9	11·4	8	10·1
1966	May	Bell Rock	Commercial Seine	874	Flag 27 5 Spaghetti 847 118	123	14·1	93	10·6
	Aug	Aberdeen	Hand Line	77	Flag	3	3·9	2	2·6
1967	Feb/Mar	Moray Firth	Commercial Seine	238	Spaghetti	24	10·1	9	3·8
	Jul/Aug	East Shetland	Commercial Seine	25	Spaghetti	0	0·0	0	0·0
	Aug	Eyemouth	Commercial Seine	988	Spaghetti	26	2·6	15	1·5
	Aug/Sep	Aberdeen	Hand Line	21	Spaghetti	1	5·0	1	5·0
1968	Aug	Moray Firth	Commercial Seine	470	Spaghetti	11	2·3	7	1·5
1969	May	Moray Firth	RV Trawl	160	Spaghetti	11	6·9	10	6·3
	Jun	Moray Firth	Hand Line	45	Flag	9	20·0	6	13·3
	Jul	Outer Moray Firth, Orkney	RV Trawl	114	Spaghetti	7	6·1	4	3·5
	Dec	Firth of Forth	RV Trawl	18	Spaghetti	0	0	0	0·0
1970	Apr	Aberdeen Bay	RV Trawl	4	Spaghetti	1	25·0	1	25·0
	May	Moray Firth	RV Trawl	6	Flag	1	16·7	0	0·0
1971	Apr	West Shetland	Commercial Seine	477	Flag	64	13·4	18	3·8
	Apr	Foula	Commercial Seine	57	Flag	0	0	0	0·0
1972	Apr	West Shetland	Commercial Seine	836	Flag	68	8·1	27	3·2
	Oct	Moray Firth	RV Seine	55	Flag	7	12·7	4	7·3

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* Up to October 31st, 1973.

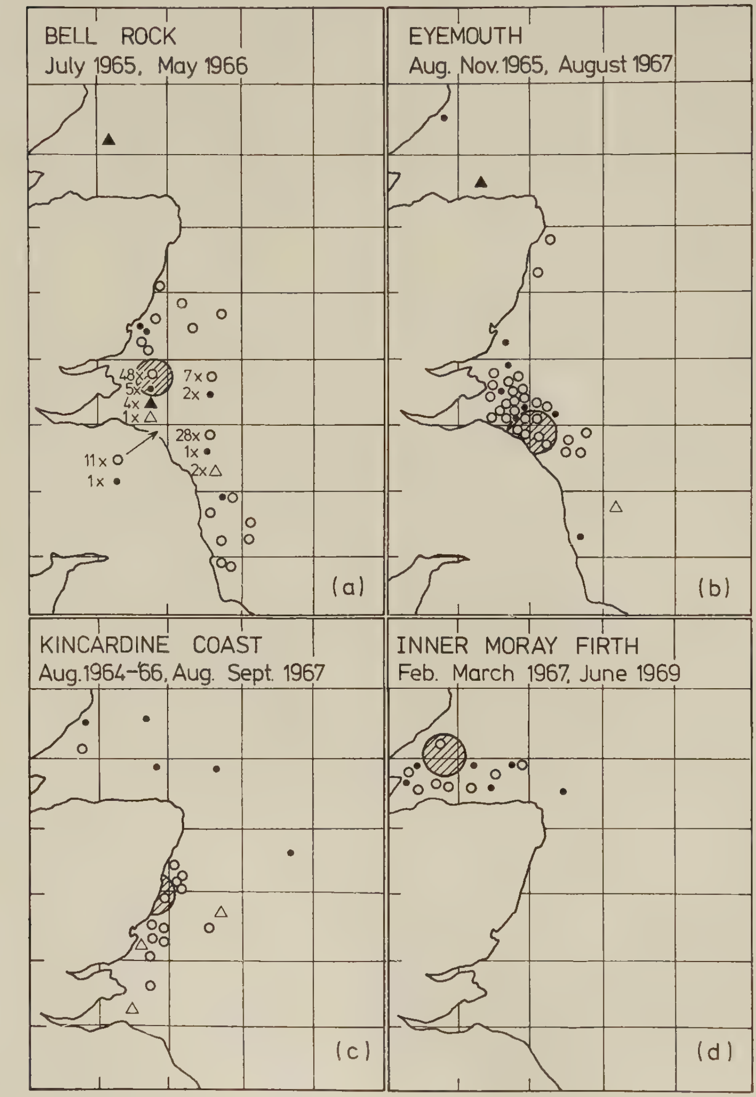


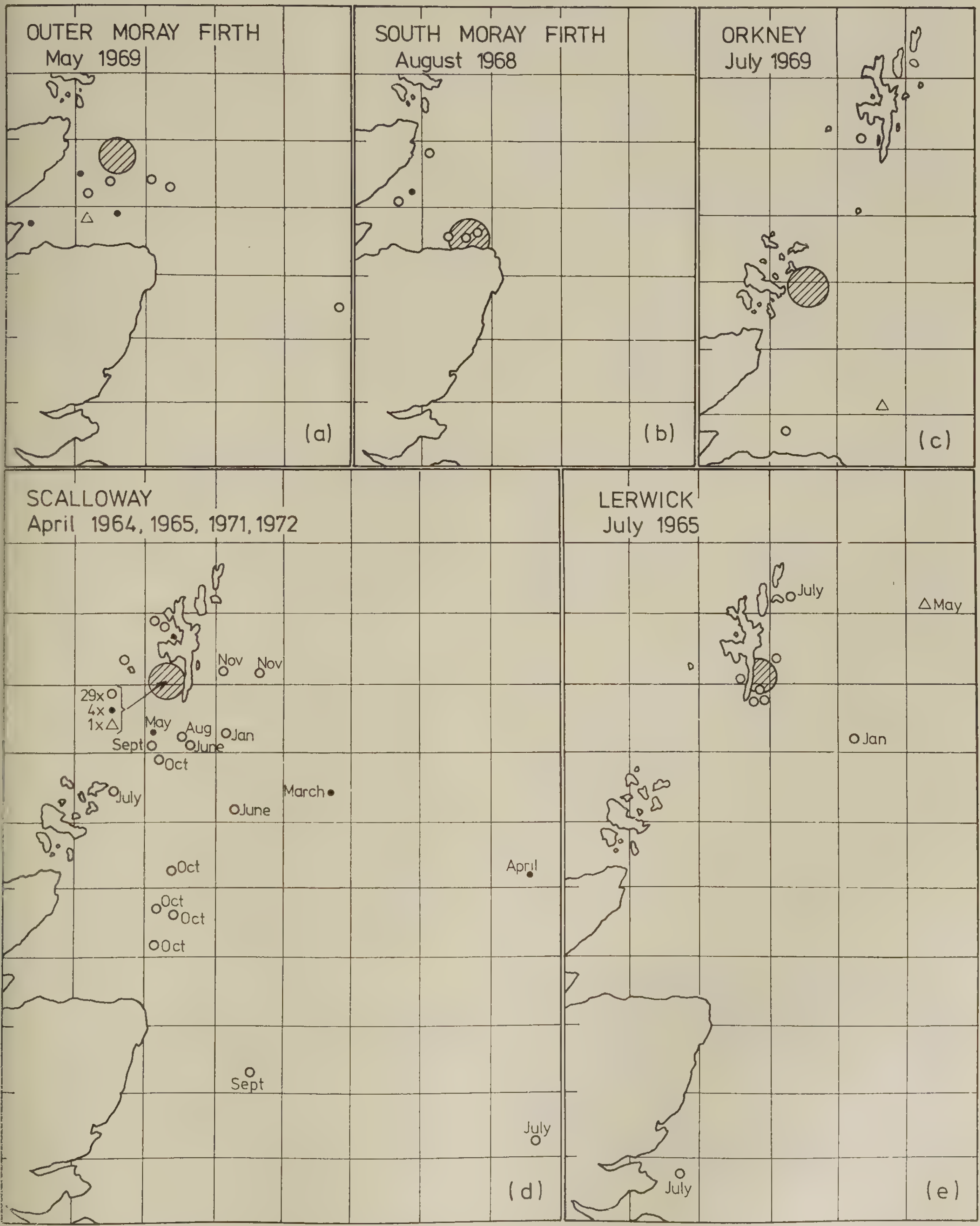
Figure 1. (a) Positions of recapture o whiting tagged in the Bell Rock are in July 1965 and May 1966. (b) Positions of recapture of whiting tagge near Eyemouth in August and November 1965 and in August 1967. (c) Pos tions of recapture of whiting tagge off the Kincardineshire coast in Au gust in the years 1964–1966 and i August/September 1967. (d) Position of recapture of whiting tagged in th inner Moray Firth in February/Marc 1967 and in June, 1969. Key: ○ Re captured June–January, absence < year. ● Recaptured February–Ma absence < 1 year. △ Recaptured June January, absence > 1 year. ▲ Recaptured February–May, absence > year. Multiple returns are indicate

In both cases the tags were attached to the fish through the dorsal musculature, between the first and second dorsal fins. There was no consistent difference between the percentage returns of the two types of tag.

The processes of capture, handling and tagging are known to cause a high initial mortality in some species. As whiting are physoclistous fish, with easily detached scales, they are very vulnerable in this respect. To reduce the likelihood of bias caused by the recapture of moribund fish, only the returns of fish that had been tagged at least 28 days previously were included in the analysis.

Results

The details of the tagging experiments are shown Table 1. In each case, the type of tag used, the relea area, the month and year of the experiment, the met od of capture and the number of fish released a recaptured are given together with the percenta recaptured. The final two columns of the Table giv in numbers and as a percentage of the fish release the returns from each experiment that were conside ed suitable for analysis. These are of fish that we recaptured after an absence of at least 28 days a from which reliable information on the date a position of recapture were obtained. Many of t experiments were on a small scale: in 15 of the


OUTER MORAY FIRTH
May 1969
(a)
SOUTH MORAY FIRTH
August 1968
(b)
ORKNEY
July 1969
(c)
SCALLOWAY
April 1964, 1965, 1971, 1972
29x ○
4x ●
1x △
May
Sept
Aug
June
Jan
Nov
Nov
Oct
July
June
March
Oct
Oct
Oct
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April
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(d)
LERWICK
July 1965
July
△May
Jan
July
(e)

Figure 2. (a) Positions of recapture of whiting tagged in the outer Moray Firth in May, 1969. (b) Positions of recapture of whiting tagged in the southeastern Moray Firth in August, 1968. (c) Positions of recapture of whiting tagged to the east of the Orkney Islands in July, 1969. (d) Positions of recapture of whiting tagged to the west of the Shetland Islands in April, in the years 1964, 1965, 1971 and 1972. (e) Positions of recapture of whiting tagged to the east of the Shetland Islands in July 1965. Keys as in Figure 1.

experiments listed, less than 100 fish were tagged. Total returns seldom exceeded 15% of releases and usable returns were considerably fewer, usually less than 10% of the fish released.

The positions of release and recapture of the whiting in these experiments are shown in Figures 1 and 2. When fish were released at the same position at similar times of the year in different years no marked year-to-year differences in the distributions of the recaptures were observed. Therefore, as the returns from individual experiments were generally few, the results of some experiments were combined. In each of the Figures a distinction is made between recaptures made during the spawning season (taken as the months of February to May, inclusive) and those made during the remainder of the year. When a fish was recaptured after an absence of more than one year, this is indicated separately.

Southeast coast of Scotland, Firths of Forth and Tay

In July 1965, 663 whiting were released close to the Bell Rock, off the Scottish east coast, giving 35 usable returns. In May 1966, a further 874 fish were released in the same area, giving another 93 usable returns. The positions of these recaptures, all from coastal waters, are shown in Figure 1a.

These results show that most recaptures made during the following spawning season were from the vicinity of the release area, although one was made in the Moray Firth. Outside the spawning season the recaptures were made mostly at positions close to, or to the south of, the release area. The data from these experiments have been analysed using the method described by Jones (1959) and the values of the parameter V (miles travelled per day) together with the mean directional components of movement, are shown in Table 2. In both experiments the mean displacement tended to be southerly. This is in contrast to the results of haddock tagging experiments in the same area, when the fish showed a generally northerly displacement (Jones, 1959).

Tagged whiting were released in the Eyemouth area, to the south of the Bell Rock, in August and November 1965, and in August 1967. A total of 1540 fish were tagged and 38 usable recaptures reported. The positions of these are shown in Figure 1b. As in the Bell Rock experiments, all the recaptures were made within coastal waters. However, it can be seen from Figure 1b that these whiting did not undertake the southerly movement shown by the Bell Rock fish: all but two recaptures were made close to, or to the north of the release area. Two returns came from the Moray Firth; both were in the spawning season and one of the fish had been at liberty for over a year.

The Eyemouth experiments took place at positions very close to those of English whiting tagging experiments described by Williams and Prime (1966) and at the same time of year. These authors also found that most of their recaptures came from inshore waters and from close to, or to the north of, the release positions, with some fish moving to the Moray Firth and its approaches.

Kincardineshire coast

During each autumn, from 1964 to 1967, a number of small experiments were conducted on whiting caught by hand-line in shallow water a few miles to the south of Aberdeen. A total of 274 fish was released, and the positions of recapture of the 22 usable returns are shown in Figure 1c. Outside the spawning season the returns were from scattered, predominantly coastal positions. Of the seven recaptures made during the spawning season, five were from positions in the approaches to the Moray Firth or in the Firth itself.

Table 2. Mean daily distance and direction travelled, for four-monthly periods, estimated from recaptures of tagged whiting liberated in the Bell Rock Area in July 1965 and May 1966

	Liberated July 1965				Liberated May 1966		
Period of recapture	Number* returned	Mean direction (°)	Mean V (miles/day)	Period of recapture	Number* returned	Mean direction (°)	Mean V (miles/day)
Feb–May	0	–	–	Feb–May	19	38	0·04
Jun–Sep	30	149	0·31	Jun–Sep	48	168	0·25
Oct–Jan	9	127	0·12	Oct–Jan	33	181	0·11
Feb–May	3	129	0·11	Feb–May	9	244	0·02
Jun–Sep	3	154	0·07	Jun–Sep	2	246	0·02
Oct–Jan	1	173	0·02	Oct–Jan	0	–	–
Feb–May	0	–	–	Feb–May	1	307	0·17

* All returns with reliable capture details have been used.

Moray Firth

The results of four experiments in the Moray Firth and its approaches are shown in Figures 1d, 2a and 2b. In all, 913 fish were released and 32 usable recaptures reported. The positions of recaptures of fish released in the inner Moray Firth in February/March 1967 and in June 1969 are shown in Figure 1d. One return was from east of the Orkneys, one from the Rattray Head region and the remainder from the southern half of the Firth itself. In May 1969, the release area was in the outer Moray Firth (Figure 2a). One return was from offshore grounds to the east of Aberdeen, the remainder coming from the Moray Firth and its approaches. Figure 2b shows the positions of recapture of whiting released close to the south coast of the Moray Firth in August 1968. The only return from outside the Moray Firth was from the Bell Rock area.

Orkneys

A small number of whiting were released to the east of the Orkneys in July 1969. The positions of recapture of the three usable returns are shown in Figure 2c. One return was from within the Moray Firth, one from its approaches and one from west of the Shetlands.

Shetlands

In April of the years 1964, 1965, 1971 and 1972 a total of 1965 whiting was released in the Burra Haaf, on the west side of the Shetlands. These fish appeared to be spawning at the time of tagging, as several of them were 'ripe and running' when released. These experiments gave 54 usable returns and their positions of recapture are shown in Figure 2d. These recaptures indicate that there was a considerable degree of dispersal from the release area after spawning, mainly in a southerly or southeasterly direction. Several returns were from the open North Sea.

In another experiment, 229 whiting were released off the east coast of the Shetlands in July 1965. The nine usable returns from this experiment are shown in Figure 2e. Two of these fish were returned from the open North Sea, one from the Bell Rock area and the remaining six from coastal waters around the Shetlands.

The cestode *Gilquinia squali* as a biological tag

Methods

The plerocercoid larva of the trypanorhynch cestode *Gilquinia squali* Fabricius, 1794, occurs in the aqueous and vitreous humours of the eye of the whiting (Fig. 3). A total of 24645 whiting of different year classes was examined for infection with this parasite in two surveys, the first from June 1964 to November 1965, and the second from April 1970 to December 1972. The sampling area lay between latitudes 55°00′N and 61°00′N and longitudes 5°00′E and 4°00′W. Samples, each consisting of from 30 to 400 whiting, were either obtained from landings at Scottish fishing ports and examined at the Marine Laboratory, or were taken by research vessels and examined at sea.

The total length of every whiting was measured to the nearest cm below. In the 1964–65 survey the sagittal otoliths of at least 50 fish from each sample, and of all infected fish from the remainder, were removed for age determination; in the 1970–72 survey, the otoliths of every fish examined were taken. All infected eyes were removed and either examined fresh or preserved in formol saline for subsequent dissection. Each plerocercoid was examined after flattening under a coverslip on a slide, to determine its stage of development. For the purposes of the present investigation the plerocercoids were divided into two groups, mature and immature. The proportions of mature plerocercoids in whiting samples may be used, on a relative basis, to determine whether infections are recent or longer established. Some information on the biology of the plerocercoid of *G. squali*, derived largely from the data from these surveys, was presented by MacKenzie (1975).

One of the features which made *G. squali* attractive as a potential biological tag was the ease with which infected whiting could be identified. At this stage no dissection is necessary apart from removal of the skin covering the eye with forceps, and it is possible for a team of two to examine up to 500 fish per day.

The majority of whiting examined in this investiga-

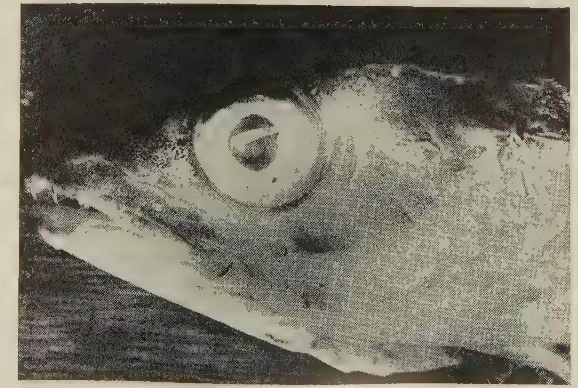

Figure 3. The pleroceroid of *Gilquinia squali* in situ in the whiting eye.

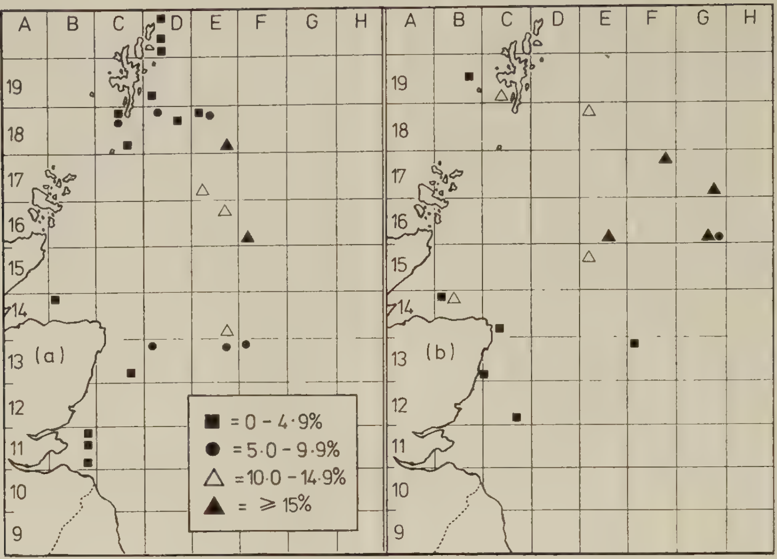

Figure 4. Incidence of *Gilquinia squali* infection in samples of the 1961 whiting year class taken in (a) June to December 1964 and (b) January to June, 1965.

tion were of three year classes: 1961, 1962 and 1967. These are considered separately below.

Results

Infections in the 1961 year class of whiting

The results of the analyses of samples of this year class taken in the two six-month periods July to December 1964 and January to June 1965 are presented separately in Figure 4, since the incidence of *G. squali* infection showed some differences between the two periods. The most striking feature of both charts was the marked difference between Scottish coastal and offshore samples. With the exception of one small sample taken in the Moray Firth in May 1965 with four out of 35 whiting infected, all coastal samples had incidence figures of less than 5%, whereas most offshore samples had more than 10% of fish infected. This offshore area of high incidence does not appear to extend south of about 57°30′N, since lower incidences were recorded in two samples from The Swatchway (statistical rectangle F13).

Four of the ten samples from the Shetlands area in 1964 were taken during a research vessel cruise in November and early December. This cruise provided an opportunity to compare the distribution of incidence of *G. squali* infection in the 1961 and 1962 year classes of whiting over a short period of time (Fig. 5). Incidence of infection in the 1961 year class to the southeast of the Shetlands was considerably lower than in the 1962 year class, and showed a progressive increase from west to east. At a number of positions, 1961 year class whiting were not taken in sufficient numbers to permit an estimate of incidence of infection to be made.

Infections in the 1962 year class of whiting

Whiting of the 1962 year class were taken in greater numbers than those of the 1961, so that Figure 6 shows a more extensive coverage than Figure 4 in both time and area. Again, the most striking feature was the difference in incidence of infection between Scottish coastal and offshore samples.

Samples taken from the three most easterly positions in November and early December 1964 ha considerably lower incidences of infection than thos from other offshore positions (Figures 5(b), 6). I particular one from statistical rectangle F16 had onl one fish infected out of 48 (2%) compared with mor than 10% in samples to the west and north. In th following period, January to June 1965, incidence o infection remained low (5%) at the most southerl of these positions (The Swatchway, F13), but ha increased to over 10% in the vicinity of the other two

From June 1964 to November 1965, 12 sample were taken from the Mithcowie/Smith Bank area o the Moray Firth (Fig. 7). In the first seven samples taken up to February 1965, the incidence of infectio remained below 7%, with a large proportion o

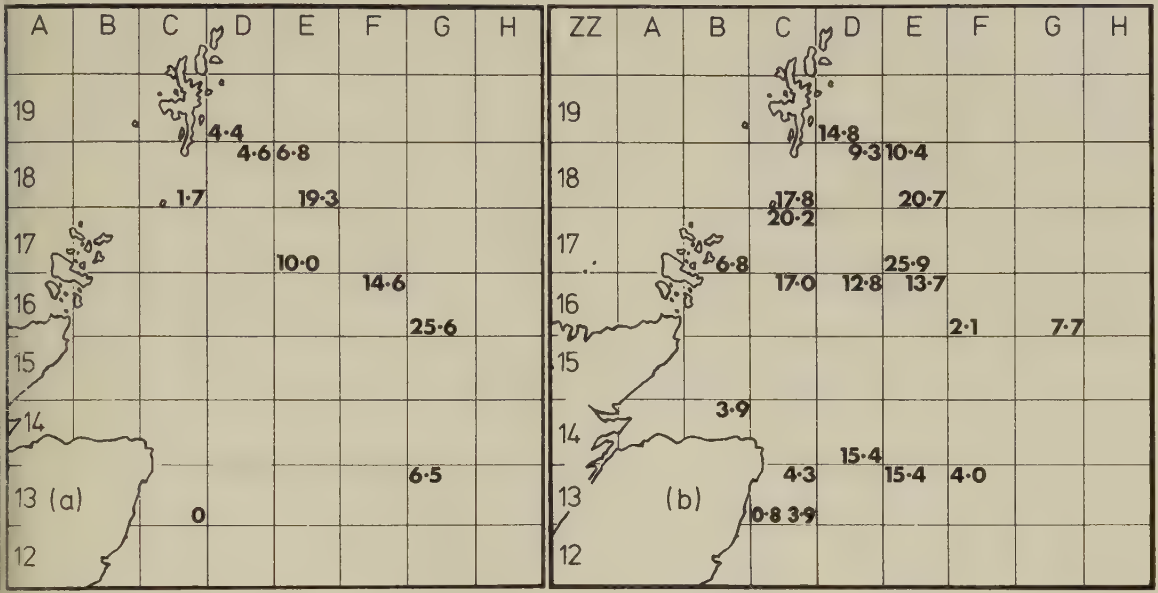
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Figure 5. Incidence of *Gilquinia squali* infection (%) in samples of (a) the 1961 and (b) the 1962 whiting year class taken in November and early December 1964. In some rectangles two or more samples were examined.

mature plerocercoids, but between the end of February and the end of May the incidence of infection increased to 18% with an accompanying decrease in maturity to zero. Since the May sample was a small one, another larger one was taken on 11 June, which confirmed the increase in incidence and decrease in maturity with figures of 15·1% and 19% respectively. From then until the end of November the incidence of infection decreased and levelled off at below 5%, while the proportion of mature plerocercoids increased to 60%. The changes in incidence over the whole period were highly significant ($P < 0{\cdot}001$).

Infections in the 1967 year class of whiting

The changes in *G. squali* infection in this year class

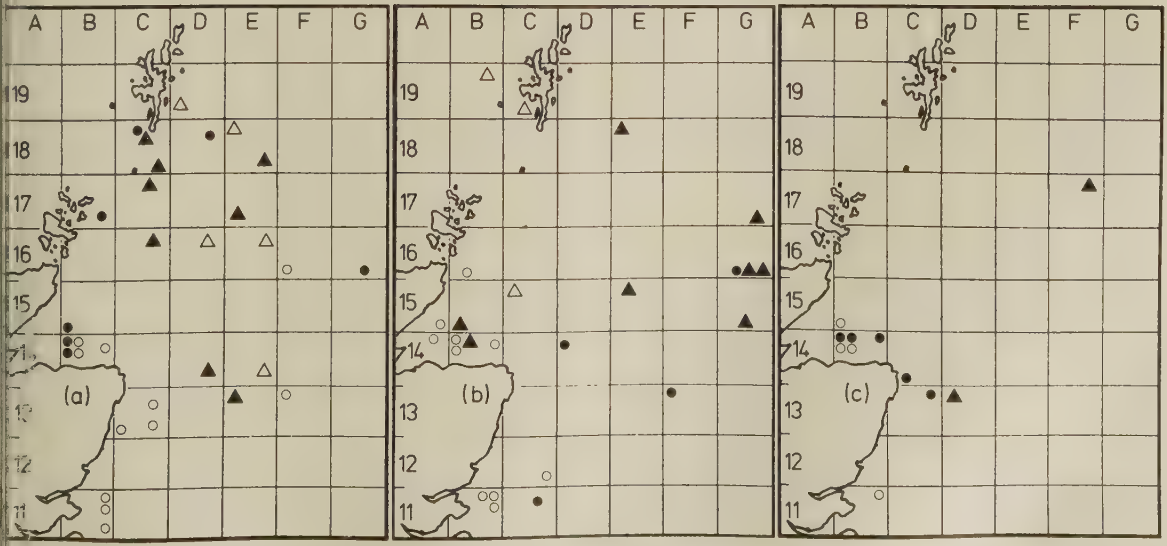
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Figure 6. Incidence of *Gilquinia squali* infection in samples of the 1962 whiting year class taken in (a) June to December 1964, (b) January to June 1965 and (c) July to November 1965. Key as in Figure 1.

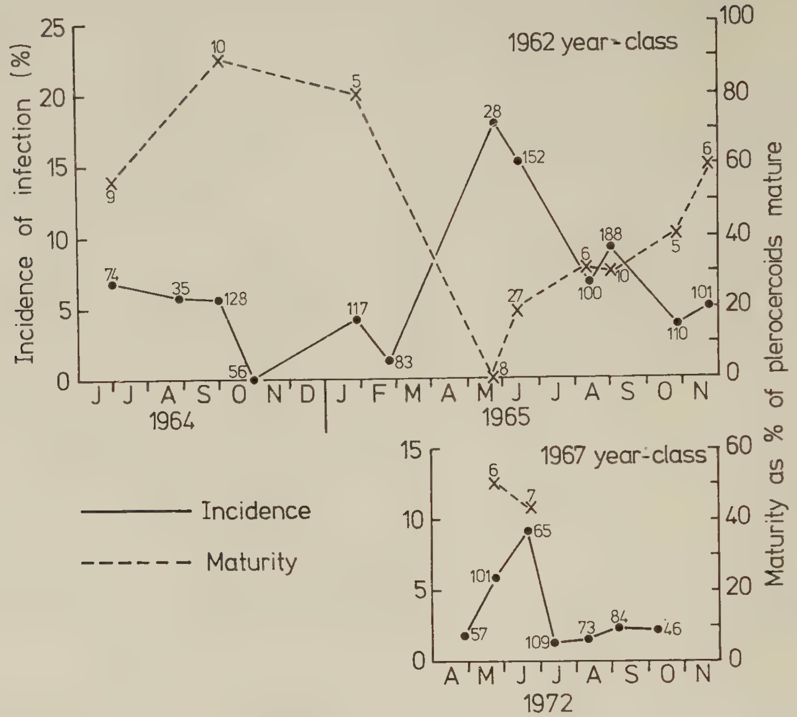

Figure 7. Variations in incidence of infection and maturity of *Gilquinia squali* plerocercoids in samples of two whiting year classes taken in the Mithcowie/ Smith Bank area of the Moray Firth. Numbers of whiting and plerocercoids examined are given.

were followed through 1970, 1971 and 1972, when the fish were 3+, 4+ and 5+ respectively (Fig. 8). During this time the incidence of infection in the study area as a whole decreased progressively from 9·4% to 2·8% (MacKenzie, 1975). During 1970 and 1971 the difference in incidence of infection between Scottish coastal and offshore samples was again apparent, but this was less marked in 1972, when one of the three samples of 5+ whiting with more than 10% incidence of infection was taken near the mainland coast, off Buchan Ness.

Up to the end of June 1971, the incidence of infection in the Shetlands area was consistently high, with mean values for each six month period of 14·4%, 10·7% and 9·2% (Fig. 9). In the period July to December 1971 this dropped significantly to 3·6% and remained at around this level until the end of the investigation. Substantial numbers of mature plerocercoids were recorded throughout.

In five samples taken from Bergen Bank (F19) from November 1970 to October 1972, the incidence of infection decreased progressively from 16·8% to 1·9%, with a greater rate of decrease subsequent to the third sample, taken in October 1971 (Fig. 10). The variations in incidence between November 1970 and October 1971 were not significant, but the decrease from October 1971 to October 1972 was significant at the 5% level. At Bressay Shoal (E17/18), about 60 miles south west of Bergen Bank, the incidence of infection remained at around 10% up to the end of the investigation.

Seven samples taken from the Mithcowie/Smith Bank area of the Moray Firth in the period April to October 1972 showed significant ($P < 0{\cdot}05$) variations in incidence of infection similar to those reported for the 1962 year class in 1965 (Fig. 7). The numbers of plerocercoids found were insufficien to show all the changes in maturity.

In January 1971, three samples of the 1967 yea class, totalling 354 whiting, were obtained from statistical rectangles J8, K8 and L8, southeast o the Dogger Bank. Only two fish (0·6%) were infected with *G. squali*.

Regional differences in incidence of infection

The analyses of *G. squali* infection data for separat year classes of whiting showed a consistent differenc

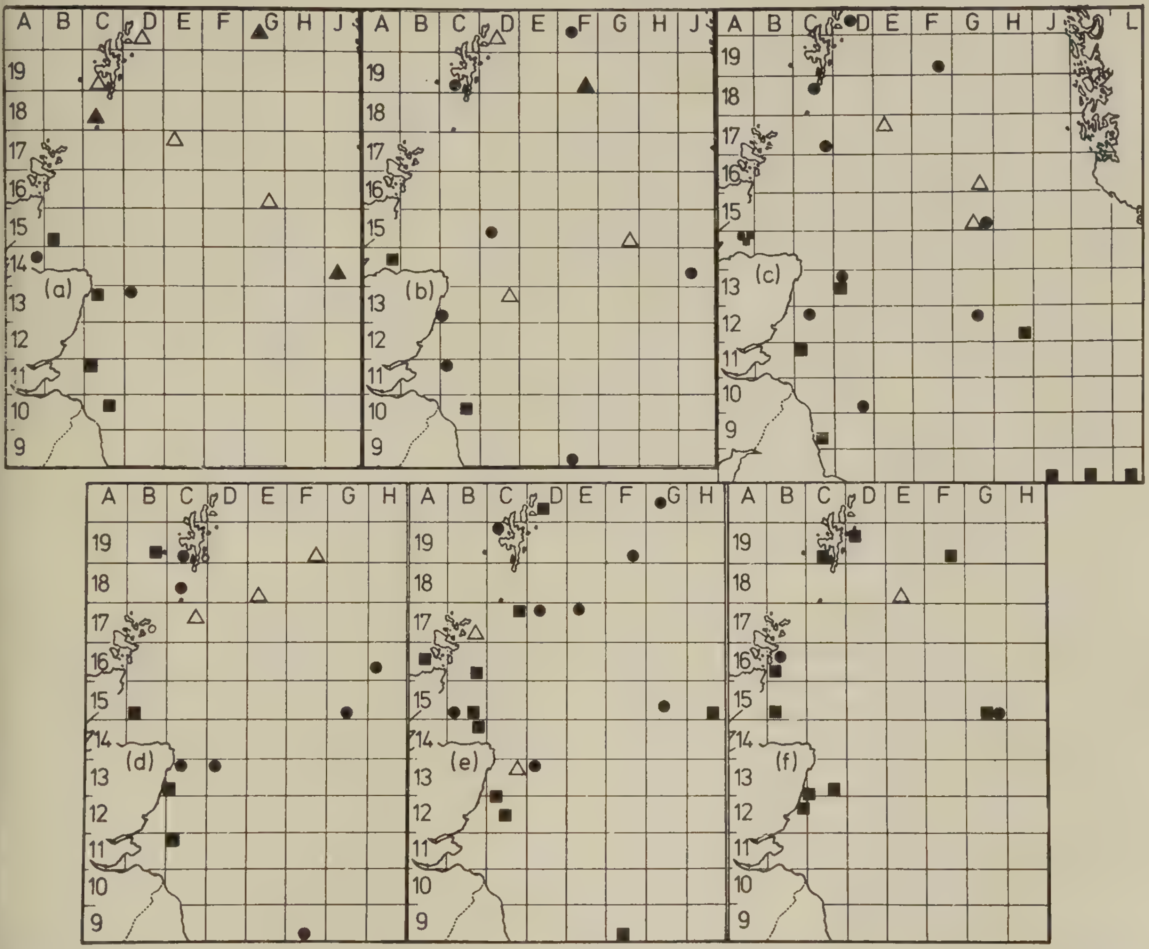

Figure 8. Incidence of *Gilquinia squali* infection (%) in samples of the 1967 whiting year class taken in six surveys during 1970 (a, b) 1971 (c, d) and 1972 (e, f). Key as in Figure 4.

between samples taken near the Scottish mainland coast and those taken on offshore grounds, while samples taken around the Shetlands showed wider variations in incidence of infection than those from other regions. The study area was therefore divided into three parts according to *G. squali* distribution (Fig. 11), and the incidence of infection in all year classes of whiting is presented separately in cm-classes for each part in Figure 12. These analyses showed that coastal and offshore whiting formed similar but non-intersecting curves of the same type as those found by MacKenzie (1975) to describe the relationship between host length and incidence of *G. squali* infection for whiting of all ages over the entire study area. In the Shetlands region, on the other hand, smaller whiting had a high incidence of infection, indistinguishable from that in offshore whiting of the same size, but this decreased sharply with length to the level of the coastal region in the largest whiting.

Discussion

Whiting tagged near the east coast of the Scottish mainland, including the Moray Firth, were recaptured predominantly within 30 miles of the coast. Although several fish were recaptured more than 100 miles from their positions of release, their directions of movement were along the coast, to north and south, rather than offshore. This was true even for those which had been at liberty for more than a year from the time of tagging. (Fig. 13). On the other hand, whiting tagged at the Shetlands were recaptured at positions more widely distributed in the northern

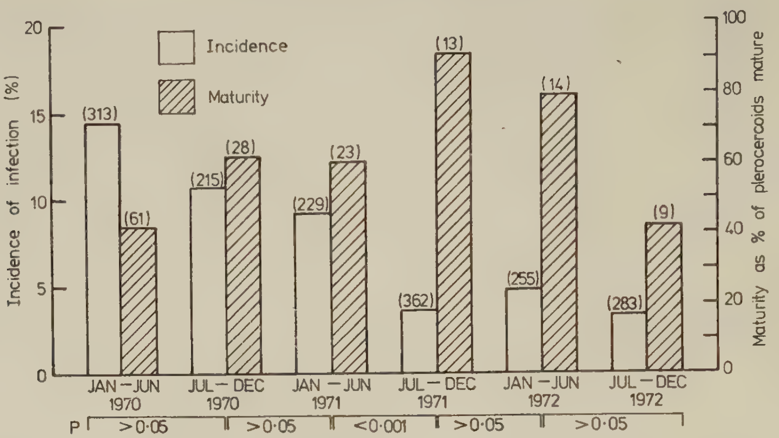

Figure 9. Variations in mean incidence and percentage maturity of *Gilquinia squali* infection from all samples of the 1967 year class taken around the Shetlands in each of six surveys. Numbers of whiting and plerocercoids examined are given; probabilities refer to differences between two consecutive mean incidence values.

North Sea, with an appreciable proportion of recaptures from offshore waters to the east and south of the Shetlands (Fig. 14). The results of the parasitological study show a marked difference in infection rate between whiting samples taken near the coast of the Scottish mainland and those taken in offshore waters of the northern North Sea. These results also show a pattern of parasitism in whiting from the Shetlands region different from that in other parts of the study area.

The greater than expected decrease in incidence of *G. squali* infection in 1967 year class whiting from the Shetlands area during 1971 suggests that the earlier whiting population of that area may have been replaced, or greatly diluted, by another with a lighter infection. The large proportion of mature plerocercoids recorded further suggests that this was not a recent infection but a long-established one. At Bergen Bank, to the east of the Shetlands, another significant decrease in incidence of infection in the same year class occurred about six months later. This suggests the possibility of a movement of whiting of ages 4+ and 5+ from west to east across this northern part of the study area. Further support for this suggestion

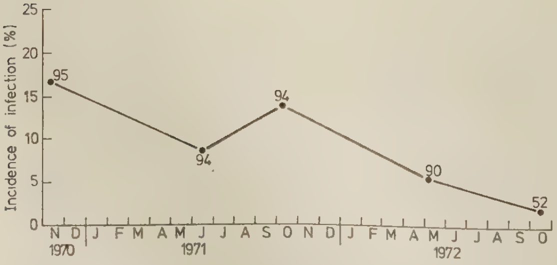

Figure 10. Variations in incidence of *Gilquinia squali* infection in samples of the 1967 whiting year class taken at Bergen Bank. Figures are numbers of whiting examined.

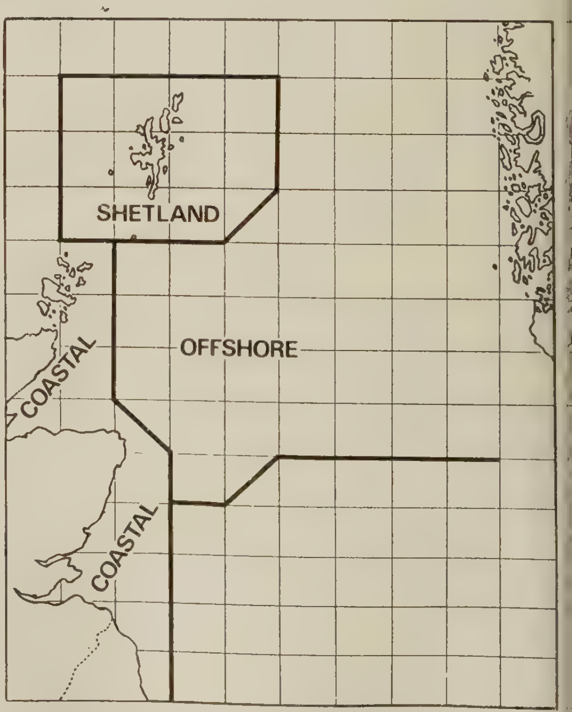

Figure 11. The study area divided into regions according to the distribution of *Gilquinia squali* in whiting.

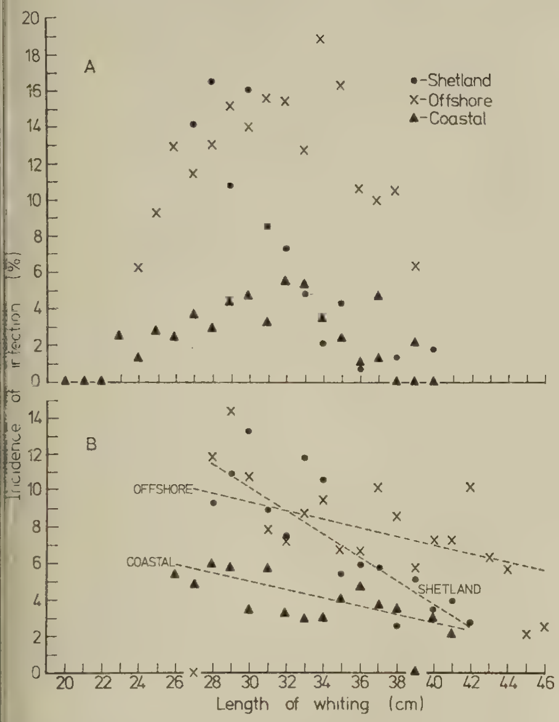

Figure 12. Relationships between incidence of *Gilquinia squali* infection and host length in regions of study area defined in Figure 11. A, all year classes of whiting examined in 1964–65; B, 1967 whiting year class examined in 1970–72.

comes from the increasing gradient of incidence of infection from west to east observed in samples of 3+ whiting of the 1961 year class in this area in November and December 1964. Finally, the analyses of regional differences in incidence of *G. squali* infection provides the strongest evidence of a movement of lightly-infected mature whiting across the Shetlands area, since the numbers involved in these analyses were so large (24645 fish). The main objection to this interpretation is that one might expect a lightly-infected migrant population to acquire the higher level of infection prevailing in their new environment. However, MacKenzie (1975) has presented substantial evidence of an immune response by whiting to *G. squali*, which appears to confer protection against further infection, as it is more evident in older fish and the incidence of infection has been shown to decrease with host age in whiting beyond the age of 3+.

The next point to be considered is the possible source of such a lightly-infected migrant group. The deep water beyond the continental shelf probably acts as an effective barrier between stocks of shallow-water demersal species, so that they are unlikely to come from the Faroes. Samples of whiting taken from off the north coast of Scotland showed that incidence of infection was low (< 5%) up to about 15 miles offshore, but beyond this it ranged from 7% to 16%, and two samples taken off Cape Wrath had more than 10% incidence of infection. This narrow coastal strip could at least contribute to the migrant population, but the most likely source appears to be the eastern coastal waters of the Scottish mainland, where whiting have been shown to have a consistently low incidence of *G. squali* infection. Since most of the tagged whiting were two or three years old when released and few were at liberty for more than a year, the tagging results do not conflict with these interpretations of the parasitological data.

The conclusion is that there is little direct migration of the younger age groups of whiting from mainland coastal waters to the offshore parts of the northern North Sea, but that some older whiting may migrate from coastal waters to the Shetlands and thence

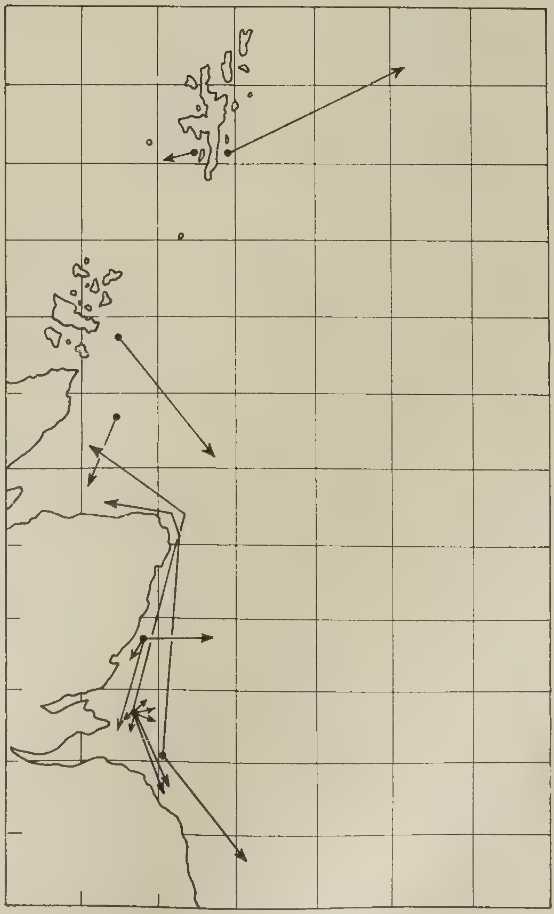

Figure 13. Movements of whiting recaptured after an absence of more than one year.

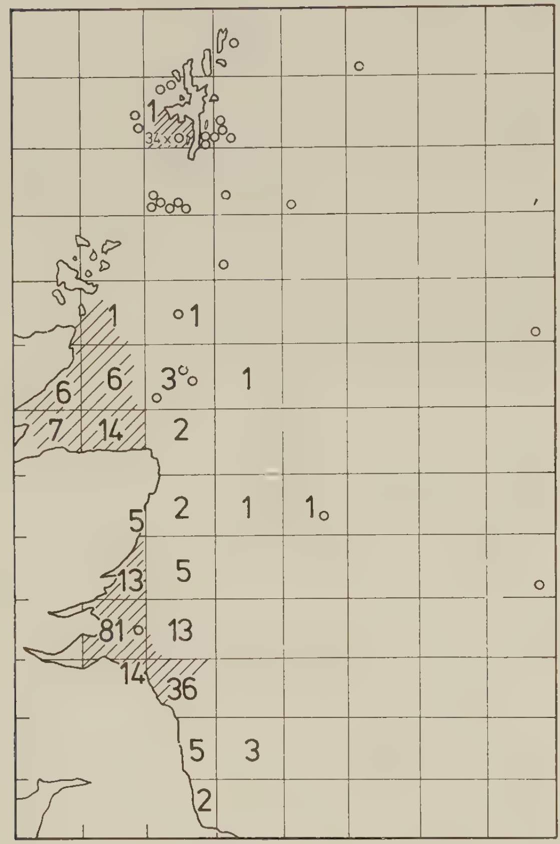

Figure 14. Distribution of recaptures of whiting tagged off the Scottish mainland (numbers of recaptures in each statistical rectangle given in numerals) and off the Shetlands (individual and multiple recaptures indicated by symbols). All experiments combined. Release areas indicated by shading.

into northern offshore waters. An age-dependant migration of this sort could account for the findings of Ellis and Jones (1956) and Gamble (1963) that commercial landings of whiting from northern North Sea offshore grounds contain a higher proportion of older fish than landings from Scottish inshore grounds.

The recaptures of whiting tagged west of the Shetlands (Fig. 2d) suggest that after spawning whiting disperse from this area in a generally southerly or southeasterly direction since, during the summer and autumn after tagging, returns came from Fair Isle, the approaches to the Moray Firth and the open North Sea. In the following spawning season, three recaptures were made in the open sea to the east of the Shetlands, which may indicate a northerly return migration to the spawning area. This result agrees with Knudsen's (1965) evidence from tagging that whiting in the northern North Sea make a northerl migration in spring followed by a southerly migration in summer. The considerable but short-live increases in incidence of *G. squali* infection observe twice in Moray Firth samples in summer may hav been the result of such a post-spawning migration

No recaptures of tagged whiting were made fron grounds off the north and west coasts of the Scottis mainland. This is in contrast to the results of taggin experiments on haddock (Jones, 1959), cod (Symonds, Pope and Raitt, in press), lemon sole (Rae 1965) and plaice (Armstrong, personal communication), in which a number of fish tagged in the sam general areas off the east coast of Scotland as in th whiting experiments were recaptured to the nort and west of Scotland. Nor were there any recapture from south of the Dogger Bank, and the incidence o *G. squali* infection in the 1967 year class was foun to be less than 1% south of the Dogger Bank at time when the mean incidence in the same year clas to the north was over 7%. These results suppo those of the earlier studies of Gamble (1959), Rou (1962), Williams and Prime (1966) and Kabata (196 that the whiting of the northern and southern part of the North Sea mix very little.

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Short Notes

Larval mortality in marine fishes and the critical period concept

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In March 1941 Soleim caught a large number of dead and decaying herring larvae in fjords and offshore areas south of Bergen on the west coast of Norway. The larvae were mainly at the yolk-sac resorption stage. Soleim (1942) concluded that he had observed a case of mass mortality in the early larval stages of the local herring.

Marr (1956) questioned Soleim's observations, inferring that the net had been contaminated with herring larvae from a previous haul. However, Marr (1956) also referred to a catch of dead newly hatched jack mackerel larvae, taken off the coast of southern California. May (1973) repeated the conclusion of Marr (1956) and rejected the observations of Soleim (1942) as unreliable.

Recently, however, Seliverstov and Penin (1974) reported the finding of dead herring larvae on the Sklinna bank off the west coast of Norway at the end of March 1969. Up to 50% of the larvae in the plankton hauls were dead, and after a storm up to 90% of the larvae taken at 0 m were dead. The stormy weather had caused the water to cool and decrease in salinity. Seliverstov and Penin concluded that the wind action was the indirect cause of the sharp decrease in the number of herring larvae observed in the investigated area (Seliverstov and Penin, 1974, p. 106–107).

In an attempt to clarify whether the observations of Soleim (1942) were correct, I recently contacted him to obtain information on his sampling techniques. (Soleim is at present curator at the Fisheries Museum in Bergen). Soleim reported that in plankton hauls taken during previous investigations he had occasionally observed herring larvae which had apparently been dead sometime before capture. There was, however, always the uncertainty that the catch had been contaminated with larvae from the previous haul. In order to avoid this problem, Soleim constructed a special plankton net (gauze No. 0, appr. 500 µm) which could be turned inside out. After a haul had been taken and the catch preserved, the net was turned inside out and a new bucket fastened to the end. The next haul was then taken with the inner surface outside, and at the following station the procedure was again repeated. In this way any contamination from a previous haul was supposed to be excluded.

At one station a very large number of dead larvae were taken in a vertical haul. A new net, which had never been used before, was then used in a surface haul, and about 100 herring larvae were caught, all dead and in various stages of decay.

Unfortunately, the technique used was not described in Soleim's paper. It should be emphasized, however, that dead and decaying herring larvae were taken in varying numbers at 9 different stations. At one station, about 800 larvae in various stages of decay were taken in a vertical haul from 50 m to the surface and only 49 larvae were alive and in a condition allowing measurement.

I hope that this note will support Mr. Soleim's previous conclusions, and that his observations will again be considered correct.

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Reviews

E. D. Goldberg (Ed.): *The Sea. Volume 5. Marine Chemistry*. John Wiley and Sons Ltd., New York, 1974, 895 pp., £ 21.70.

After the devotion of the previous two volumes of *The Sea* to the geology of the sea floor, it comes as something of a relief to find that marine chemistry is dealt with in one volume. It is a tribute to Professor Goldberg and his editorial board that they have managed to confine the rapidly expanding subject of seawater chemistry to one book. Needless to say, the present volume is long, massive (almost 1·8 kg) and, seemingly inevitably, expensive.

The book is dedicated to the late Professor Lars Gunnar Sillén, one of the foremost inorganic chemists of this century who, during the latter years of his life, applied himself to the task of trying to understand the chemistry of sea water. It is most fitting that a major work in marine chemistry, such as *The Sea* Vol. 5, should honour Sillén, because his input to the field has had profound results. By considering the water and sediments in the ocean as a chemical system at equilibrium, an overall model for seawater chemistry was established, against which the field observations could be tested. In some cases the model and field data are in agreement, but in many instances they are not. The real power of the approach is that it enables the ultimate state of the system to be predicted. Discrepancies between the observed and final states for particular components can then be attributed to kinetic/biological effects which are thus identified as worthy of further study. In this way chemical oceanography becomes less an open ended data gathering exercise and more a rigorous branch of chemistry.

The book contains 23 individual chapters subdivided into 6 parts. The first part consists of five chapters under the general title 'Thermodynamics of the Seawater System'. In 'Seawater as a Multicomponent Electrolyte Solution', F. J. Millero reviews physico-chemical approaches to ion-ion interactions in single and multicomponent electrolyte solutions. These ideas are then applied to prediction of the properties (volume, thermal and transport) of sea water and of solutes in the medium of sea water (e.g. activity coefficients, partial molal volumes and enthalpies). There is little mention of explicit sea water models, such as the ion association approach of Garrels and Thompson and that involving specific ionic interaction proposed by Whitfield. In the next chapter A. Disteche examines the effects of pressure on ionic equilibria in sea water. The partial molar volume and dissociation/association constant approaches are used to investigate the effect of pressure on the sulphate and carbonate systems in ocean waters. In 'The Alkalinity–Total Carbon Dioxide System in Seawater' J. M. Gieskes presents a workmanlike synthesis of ideas from chemistry, physical oceanography, marine geology and biology as they affect the oceanic carbonate system. After a brief review of the thermodynamics of the system (which summarises a number of the points made in the previous two articles) topics covered include the distribution of alkalinity and total CO_2 in the oceans, sedimentation and dissolution of calcium carbonate and exchange of carbon dioxide across the air-sea interface. In his equilibrium model of the oceans Sillén assumed that the redox potential was controlled by the O_2/H_2O couple and used a value for the pE of 12·5. This led to problems with the speciation of a number of elements (e.g. N, I, Mn). W. G. Breck in his chapter 'Redox Levels in the Sea' elaborates on the idea that the operative redox potential in sea water is poised by the O_2/H_2O_2 couple, leading to a lower value than used by Sillén. With a lower value for pE many of the multivalent elements cease to present problems. In the final article in this part of the book D. Dyrssen and M. Wedborg present an updated and extended version of the sort of equilibrium calculations of the speciation of elements in seawater used in the Sillén model.

Part II contains three chapters concerned with air-sea interactions. R. H. Bieri discusses the results of oceanic measurements of dissolved noble gases. Some studies appear to show deviations from equilibrium for these gases between the atmosphere and the ocean across the air-sea interface. However, the lack of agreement between the methods used by different workers to measure noble gas concentrations makes interpretation of the data extremely difficult. As shown by W. Seiler and U. Schmidt in their chapter, the situation is somewhat easier for some nonconservative gases which can show considerable supersaturation in surface sea water. In the last chapter 'Chemical Fractionation and Sea-Surface Microlayer Processes', F. MacIntyre presents an original, and at times amusing, approach to the processes occurring at the very surface of the sea, with especial reference to the fractionation which has often been reported for elements traversing the air-sea interface. From a critical assessment of the available data, MacIntyre concludes that for very few elements has such fractionation been unequivocally demonstrated.

The longest Part (III) of the book is concerned with the sedimentary cycle and consists of nine chapters. In the first of these R. M. Garrels and E. A. Perry develop a steady-state model for the cycling of the elements carbon, sulphur and oxygen in the sediment-ocean-atmosphere system over the last 600 million years. Over this time period the composition of the ocean and atmosphere is argued to have been appreciably constant, but transfer between mineral reservoirs has probably occurred. From their analysis the authors conclude that the rate of photosynthesis is proportional to the amount of carbon dioxide in the atmosphere and that this is probably the main mechanism maintaining the constant composition of both atmosphere and oceans. The next two chapters, entitled 'The Magnesium Problem' (J. I. Drever) and 'The Silicon Problem' (R. Wollast), are essentially concerned with input-output budgets for these two elements in the ocean system. In both cases it appears that the input to the ocean (mainly from freshwater inflow) is too great to be accounted for by well established removal processes. In the case of magnesium Drever argues that the most likely explanation for the discrepancy is because the present-day magnesium flux in rivers is unrepresentative of conditions in the past. For silicon, Wollast favours the reaction of dissolved silicon with clay minerals in marine sediments. Only a small amount of data is presented to support this conclusion and unfortunately there is no cross-referencing to additional evidence in a subsequent chapter by Manheim and Sayles. Of the next three chapters, two are primarily concerned with the use of isotope techniques in marine chemistry. G. D. Garlick reviews the use of stable isotopes of oxygen, carbon and hydrogen, and E. D. Goldberg and K. Bruland provide a much needed critical account of radioactive techniques used for dating marine sediments. A chapter by R. A. Berner dealing with kinetic models for the early diagenesis of nitrogen, sulphur, phosphorus and silicon in anoxic sediments is sandwiched rather uncomfortably between the two articles on techniques. Next comes a chapter by D. S. Cronan on 'Authigenic Minerals in Deep-Sea Sediments'. In this the main classes of minerals found in the oceans, including manganese nodules, are described in terms of crystal structure, chemical composition and geographic distribution, with some discussion of their modes of formation. In 'Composition and Origin of Interstitial Waters of Marine Sediments, Based on Deep-Sea Drill Cores' F. T. Manheim and F. L. Sayles have done a very useful job in summarising the interstitial water results from the Deep Sea Drilling Project. The final chapter in this part of the book is a lengthy, authoritative account of the sulphur cycle in the marine environment (M. B. Goldhaber and I. R. Kaplan).

The fourth part has the general title 'The Impact of Life Processes Excluding Man' and contains three chapters. The first is a well reasoned and thought provoking look by D. W. Menzel at primary production and the origin of dissolved and particulate organic carbon in the oceans. Menzel goes on to argue that very little oxidation of dead organic material occurs below a depth of a few hundred metres. In 'Natural Products Chemistry of the Marine Environment' D. J. Faulkner and R. J. Anderson catalogue 194 different compounds which have been isolated from marine organisms. The authors are obviously writing on a topic which involves presentation of a lot of factual material but the unfortunate reader is not helped by the total absence of any division of the text into sections. H. A. Lowenstam writes on the intriguing topic 'Impact of Life on Chemical and Physical Processes'. Most marine chemists would argue that life has a profound effect on the chemistry of sea water, but its role in physical processes is harder to see. The apparent problem arises because by 'physical' the author does not mean the gamut of processes from ocean circulation to salt fingering studied by physical oceanographers, but rather the incorporation of chemicals into the hard parts of organisms.

Part five is concerned with the impact of man on the chemistry of the oceans. It contains only two chapters ('Heavy Metals, Metalloids and Synthetic Organics' by A. Jernelov and 'Artificial Radioactivity in the Sea' by A. Preston) and it is arguable that it should have been omitted. The topic is large and to do it justice (as in 'Impingement of Man on the Oceans' ed. by D. W. Hood) much space is required. The 37 pages in the present volume are clearly inadequate and the situation is made even worse because Jernelov's chapter is very inadequately referenced.

The book's final section has but one chapter entitled 'Origin of the Ocean' by G. Arrhenius et al. The authors argue against the idea that the ocean and atmosphere developed only after the solid earth had formed and for the view that the processes which led to formation of the earth contemporaneously played a decisive role in the differentiation which produced the precursors of the present ocean and atmosphere. It is a pity that the authors do not go on to discuss the history of sea water from its beginning up to recent times. This topic is covered, in part, in the chapter by Garrels and Perry but since it is so fundamental to Sillén's ideas it really deserves a more extended treatment.

Viewing the book as a whole one cannot fail to be impressed by the high standard of the majority of the chapters. Obviously in a multi-author book there will be some articles which could have been better, but on the whole Prof. Goldberg and his editorial board have chosen their authors well. It is also refreshing to find that the ratio of non-U.S. to U.S. authors (12:22) is high relative to many other scientific texts, and probably truly reflects the achievements in the field.

On the debit side there is a dearth of cross-referencing between chapters and the reference list for at least one chapter is in bad need of correction and updating. Cross-referencing is important in a book with a large number of authors because it not only helps the reader to pick out underlying themes in the subject but also increases the comprehensiveness of individual chapters. Inevitably some topics are not covered in any depth (e.g. the effect of biological processes on nutrient distributions both with depth and horizontally, trace metals, analytical chemistry of sea water, mixing models, coastal waters, estuaries and fjords). The weighting of different parts turns out rather strangely. As already mentioned, the parts on pollution and the origin of the oceans are too brief, while in the three chapters concerned with air-sea interaction little or nothing is said about some of the most important gases e.g. O_2, CO_2, SO_2. In contrast, Part IV on the sedimentary cycle is unnecessarily long due to the inclusion of two chapters on isotope techniques. A number of the longer chapters would probably have benefited from some compression.

This is certainly a book which every institution in which the study of marine chemistry is pursued must have in its library. It is a great pity that the price will certainly deter many researchers from purchasing a copy for themselves. The publishers presumably cost and price books of this sort on the basis that sales to libraries will constitute the bulk of the copies sold. It would be interesting to know why the publishers do not introduce a dual pricing system for important scientific texts. This system, in which individuals (the libraries of whose institutions buy the book at full price) can purchase it direct from the publishers at a substantially reduced price, is already operated for many scientific journals. In the present case such a pricing policy would enable individual marine chemists to have, at a reasonable cost, a copy of a book to which, because it is the most comprehensive and important one volume text on the topic, they must have access.

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George A. Rounsefell: Ecology, utilization and management of marine fisheries. C. V. Mosby, St. Louis, 1975. 516 pp. $ 26.25.

This text is more than a replacement of Rounsefell and Everhart's book published in 1953; it summarizes much work done since that date. A short historical introduction lists the founding fathers and their successors; an encomium on Dr W. B. Chapman ends: "allowing our foreign fishery policies to be run almost wholly by the larger tuna corporations (who employed him) . . . . . has resulted in our present position as a second rate fishing nation". The conclusion is wrong and Dr. Chapman's overwhelming and powerful concern was for all fisheries.

The text proper starts with a short description of the physical environment. The distributions of the current systems are presented on South Pole projections which I found unfamiliar, indeed disconcerting. It is essentially a geographical description; I have learned a new word, *exorheic*, which means that the fresh water input to a sea exceeds the evaporation. The primary biological environment is described in terms of the forms of upwelling and the inputs of nutrient into the system.

There are two chapters on limiting factors, physical and biological. Oxygen, salinity and temperature are shown to have particular effects at extremes. The biological factors are the red tides, predation and competition, each of which is a large subject treated very briefly. It is a truism that any population must become limited, but if "limiting factors" are examined in isolation their effects appear only to be shown in the extreme; yet the population is controlled in the middle ranges.

There is a very good description of fisheries throughout the world based on the FAO Tables fo 1968. Catches by families and species are grouped a cold, cool, warm and tropical. The value of US catches by species is tabulated for 1967. The pe capita consumption is given by countries. The in crease in catches by countries is shown between 1950 and 1971 and a study is developed of the potential world catches. It is based on the estimates in upwelling areas given by Ryther and myself, which the author improves. But there is no reference to Gulland's *Fish Resources of the Ocean* (1972), which is the authoritative statement of potential world catches and shows that they may be limited to about 100 million tons.

The United States Fisheries are described very fully in a subsequent chapter. It is followed by one on gear, a very complete and up-to-date one. In particular the illustrations are remarkable; they were mainly drawn by S. G. Duran for various publications of the former US Fish and Wildlife Service.

Natural fluctuations in abundance are described in examples of long term series, Karluk river sockeye, albacore, mackerel and lobsters. Some are roughly correlated with changes in air temperature or in salinity. There is little conclusion from this chapter, but the scale of variability is clearly shown.

The unity of populations is discussed in terms of parasites, morphometric material, differences in age distributions, in growth and in returns from marking experiments. They are all techniques that may or may not provide differences between populations, but there is no discussion of what constitutes the unity of a population. There is only a short paragraph on genetics, but no discussion of its uses in population studies.

There is a chapter on population dynamics, on direct counts, marking experiments, egg and larval sampling, acoustic survey and a discussion of a paper by Widrig, some twenty years old. However, the chapter is unsatisfactory, if there is little wrong with it; the trouble is that there is no attempt to describe the population structure. Perhaps as a consequence, the chapter on management is also a little old fashioned. Selectivity, closed areas and quotas are described together with the need to reduce fishing mortality. In the introduction Professor Rounsefell discards the maximum sustainable yield on economic grounds in accordance with current American thought.

The maximum sustainable yield is a catch taken perhaps at some economic strain. However, to discard it is to miss the point. Before we act, it must be determined because the best economic yield is taken at a fraction of the MSY, and therefore it should not be discarded. It has become a Holy Grail, as unattainable. This point is an essential one for management, not discussed in this book.

There follow chapters on engineering projects, on commercial culture and on the life histories of commercial fishes. There is a glossary and a list of little known places.

There are many potential text books on fisheries science. This one in particular is based very largely on Professor Rounsefell's experience, much of which has not been recounted elsewhere. Other texts might deal with population dynamics (for example) more fully, but this one has a historical taste which stems from Rounsefell's very successful life as a fisheries research worker.

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Relationship between total ammonia and free ammonia in terrestrial and ocean waters

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The toxic effects of ammonia to fish are generally considered to be caused by the unionized fraction (NH_3), rather than by the ionic components (NH_4^+ and $NH_4SO_4^-$), which co-exist in equilibria in ammonia-in-water systems. The equilibrium is highly dependent on pH, temperature, pressure and ionic concentrations. The physico-chemical parameters of the system have been evaluated by Whitfield (1974) for most conditions encountered in terrestrial and ocean waters, including fish rearing situations. This note describes a computer program which has been written for easy, routine but precise calculation of the unionized ammonia fractions.

Whitfield, M. 1974. J. mar. biol. Ass. U.K., 54: 562–80.

Introduction

n fish farming the toxic aspect of ammonia to fish of primary concern. The total ammonia concenration, ($[NH_3] + [NH_4^+] + [NH_4SO_4^-]$) is also elevant as a nutrient to simple organisms in the acterial filters in fish tanks, and at the subordinate evels supporting the higher trophic levels in large ale fish farming e.g. in enclosed lochs. The toxic ffects are exercised by the free ammonia [NH_3], his being the entity which can rapidly penetrate cell embranes via the lipoidal segments. (Lloyd and erbert, 1960; Fromm and Gillotte, 1968; Meyer nd Winkelmann, 1969; Tabacs and Holt, 1971; nd Gulik-Kzywicki, 1975). The equilibrium

$$NH_4^+ + H_2O \rightleftharpoons NH_3 + H_3O^+$$

nd hence the proportion occurring as free ammonia, extremely dependent on pH and other conditions emperature, pressure, ionic concentrations etc), articularly in the range of these parameters encounered in natural fresh and saline waters.

Whitfield (1974) has made a precise and detailed valuation of the effects of these variables on the roportion of free ammonia (NH_3). The stability onstant of this reaction is

$$K_a{}^0 = ([NH_3]\,[H^+] / [NH_4^+]) \times \\ \times (\gamma_{NH3} \cdot \gamma_{H^+} / \gamma_{NH4^+} + a\,H_2O)$$

here a_x, $[X]$ and γ_x represent the activity, the conentration and the activity coefficient of component respectively.

A convenient representation applicable to saline waters is given by the expression:

$$\log K_a{}^s = \log K_a{}^0 - \log \Gamma_a{}^s$$

with $K_a{}^s = [NH_3]\,[H^+] / [NH_4^+]$ where $K_a{}^s$ is a stoichiometric constant and $\Gamma_a{}^s = \gamma_{NH3} \cdot \gamma_{H^+} / \gamma_{NH4^+} + a\,H_2O$ where $\Gamma_a{}^s$ is an activity quotient at the particular temperature, pressure and ionic concentrations.

Whitfield has provided a set of empirical equations representing the hydrolysis constant of ammonium ions in sea water, $pK_a{}^s$, at any pressure P (atmos.), temperature T (K), and salinity S (‰), indicating the molal ionic strength, I, likely to be encountered in all marine waters. The value of $K_a{}^0$, acid stability constant at zero ionic strength, determined by Bates and Pinching (1949), has been used.

Estimates of free ammonia are not readily obtained directly by electrode measurements using ammonia gas permeable membranes because of interferences from other gases present, (CO_2 etc); these interferences are serious in the pH range of natural waters. Total ammonia measurements can of course be made with such electrodes when used in waters having appropriate controlled solution conditions. In order to apply these measurements to the routine monitoring of fish tanks or ponds for ammonia, and in other fields in which routine ammonia measurements are involved or in modelling artificial nutrient systems, a Fortran computer program has been compiled, and used to process batches of the relevant data (total ammonia and the other

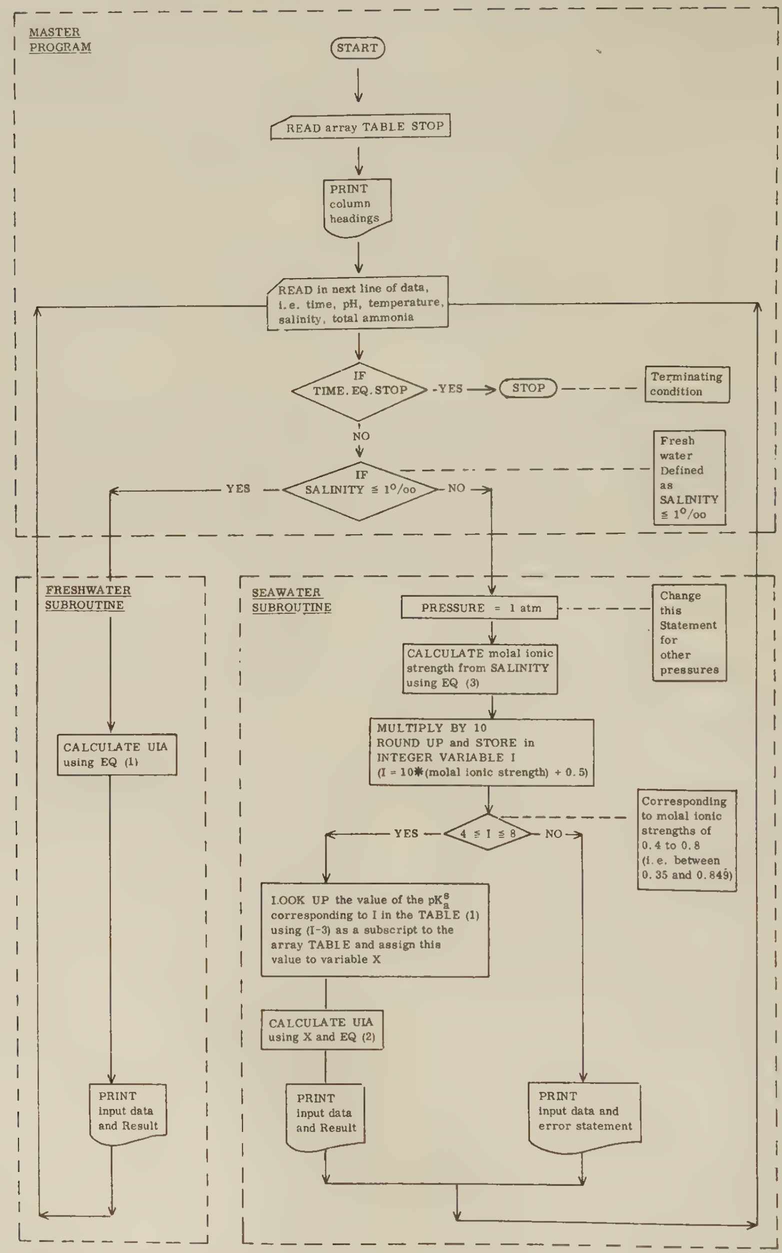

MASTER PROGRAM
START
READ array TABLE STOP
PRINT column headings
READ in next line of data, i.e. time, pH, temperature, salinity, total ammonia
IF TIME. EQ. STOP
YES
STOP
Terminating condition
NO
IF SALINITY ≤ 1°/oo
YES
NO
Fresh water Defined as SALINITY ≤ 1°/oo
FRESHWATER SUBROUTINE
CALCULATE UIA using EQ (1)
PRINT input data and Result
SEAWATER SUBROUTINE
PRESSURE = 1 atm
Change this Statement for other pressures
CALCULATE molal ionic strength from SALINITY using EQ (3)
MULTIPLY BY 10 ROUND UP and STORE in INTEGER VARIABLE I (I = 10*(molal ionic strength) + 0.5)
4 ≤ I ≤ 8
YES
NO
Corresponding to molal ionic strengths of 0.4 to 0.8 (i.e. between 0.35 and 0.849)
LOOK UP the value of the pK^s_a corresponding to I in the TABLE (1) using (I-3) as a subscript to the array TABLE and assign this value to variable X
CALCULATE UIA using X and EQ (2)
PRINT input data and Result
PRINT input data and error statement

Figure 1. Flow scheme for computer evaluation of the occurrence of unionized ammonia in fresh or sea water at varying pH, temperature, salinity and pressure.

variables) to give accurate estimates of the free ammonia concentration in a simple manner. The program (filed at Lowestoft) is illustrated as a flow diagram on Figure 1. It is listed in Figure 2, with formats for input of data and output shown in Figure 3. The latter shows typical data selected from the daily measurements of an experiment in which young trout were reared in freshwater, which w then changed to sea water. The program incorporat sub-routines dealing with the physical chemistry the seawater and freshwater situations respective appropriately selected by the master program the basis of salinity.

```
       MASTER ANON8
       INTEGER TIME,STOP
       DIMENSION TABLE(5)
       READ(5,1)TABLE,STOP
 1     FORMAT(5F4.2,A4)
       WRITE(6,2)
 2     FORMAT(1H ,9HTIME FROM,4X,2HPH,7X,11HTEMPERATURE,5X,8HSALINITY,7X,
      113HTOTAL AMMONIA,16X,17HUNIONIZED AMMONIA/1H ,8HSTART OF,18X,3H(K)
      2,9X,10H(P.P.THOU),3X,7H(P.P.M),3X,9HMICRO G N,7X,7H(P.P.M),3X,9HMI
      3CRO G N,5X,10HPERCENT OF/1H ,10HEXPERIMENT,51X,7HATOMS/L,19X,7HATO
      4MS/L,9X,5HTOTAL/1H ,102X,7HAMMONIA)
12     READ(5,10)TIME,PH,TEMP,SALIN,TOTAM1
10     FORMAT(A6,F6.3,F5.1,F7.4,F6.3)
       IF(TIME.EQ.STOP)GOTO 15
       IF(SALIN.LE.1.0)GOTO 16
       CALL SEAWATER(TIME,PH,TEMP,SALIN,TOTAM1,TABLE)
       GOTO 12
16     CALL FRESHWATER(TIME,PH,TEMP,SALIN,TOTAM1)
       GOTO 12
15     STOP
       END

END OF SEGMENT, LENGTH   85, NAME ANON8
```

```
       SUBROUTINE SEAWATER(TIME,PH,TEMP,SALIN,TOTAM1,TABLE)
       INTEGER TIME
       DIMENSION TABLE(5)
C      TO USE THIS PROGRAM AT OTHER PRESSURES, CHANGE NEXT STATEMENT
       PRESS=1.0
       TOTAM2=TOTAM1/0.014008
       I=10.0*(19.9273*SALIN/(1000.0-1.005109*SALIN))+.5
       IF(I.LT.4)GOTO 13
       IF(I.GT.8)GOTO 13
       X=TABLE(I-3)
       FREAM1=TOTAM1/(1.0+10.**(X+.0324*(298.-TEMP)+.0415*PRESS/TEMP-PH))
       FREAM2=FREAM1/0.014008
       FREAM3=100.0/(1.0+10.**(X+.0324*(298.0-TEMP)+.0415*PRESS/TEMP-PH))
       WRITE(6,11)TIME,PH,TEMP,SALIN,TOTAM1,TOTAM2,FREAM1,FREAM2,FREAM3
11     FORMAT(1H ,A6,6X,F6.3,6X,F5.1,9X,F7.4,6X,F6.3,5X,F6.1,9X,F9.6,1X,
      1F9.3,6X,F9.5)
       GOTO 18
13     WRITE(6,14)TIME,PH,TEMP,SALIN,TOTAM1,TOTAM2
14     FORMAT(1H ,3A2,6X,F6.3,6X,F5.1,9X,F7.4,6X,F6.3,5X,F6.1,12X,23HDONT
      1EAT THE FISH TODAY)
18     RETURN
       STOP
       END

END OF SEGMENT, LENGTH   177, NAME  SEAWATER
```

```
       SUBROUTINE FRESHWATER(TIME,PH,TEMP,SALIN,TOTAM1)
       INTEGER TIME
       TOTAM2=TOTAM1/0.014008
       FREAM1=TOTAM1/(1.0+10.0**(18.915-.0324*TEMP-PH))
       FREAM2=FREAM1/0.014008
       FREAM3=100.0/(1.0+10.0**(18.915-0.0324*TEMP-PH))
       WRITE(6,17)TIME,PH,TEMP,SALIN,TOTAM1,TOTAM2,FREAM1,FREAM2,FREAM3
17     FORMAT(1H ,3A2,6X,F6.3,6X,F5.1,9X,F7.4,6X,F6.3,5X,F6.1,9X,F9.6,1X,
      1F9.3,6X,F9.5)
       RETURN
       STOP
       END

END OF SEGMENT, LENGTH   85, NAME  FRESHWATER
```

Figure 2. Computer program for calculation of the percentage of unionized ammonia comprising master program and subroutines for freshwater and sea water conditions.

Application to deep ocean water

The equations on which the program is based incorporate Whitfield's (1974) expressions for the pH, temperature, pressure and ionic strength effects on the ionization of ammonia, so as to calculate the unionized ammonia fraction throughout the ranges of all these variables encountered in the ocean. However, the listing and data input formats shown (Figs 2 and 3) are in a form convenient to avoid the unnecessary input of pressure data when all measurements relate to pressures at around 1 atmosphere, as is the case in fish rearing work and in terrestrial waters and shallow seas (e.g. to 100 m). For use at a different fixed pressure the statement PRESS = 1·0 is changed to the appropriate pressure in atmospheres. When the program is applied to situations where a series of ammonia measurements refer to differing pressures, as in deep water oceanography, the following modifications to the listing are made.

MASTER PROGRAM

Line 12;

```
12    READ (5, 10) TIME- - - - - - - - - - -
```

the variable PRESS is added at the end of this read list

```
i.e. 12    READ (5, 10) TIME, PH, TEMP, SALIN,
           TOTAM1, PRESS
```

Line 13;

```
10    FORMAT (A6 - - - - - - - - - - -
```

the format F5.0 is added to the end of the list

```
i.e. 10    FORMAT (A6,F6.3,F5.1,F7.4,F6.3,F5.0)
```

Line 16;

```
      CALL SEAWATER - - - - - - - - - - -
```

the variable PRESS is added to the end of list of arguments

```
i.e.  CALL SEAWATER (TIME, PH, TEMP,
      SALIN, TOTAM1, TABLE, PRESS)
```

SUBROUTINE SEAWATER

Line 1;

```
      SUBROUTINE SEAWATER - - - - - - -
```

PRESS is added to the end of list of arguments

```
i.e.  SUBROUTINE SEAWATER (TIME,
      PH, TEMP, SALIN, TOTAM1, TABLE
      PRESS)
```

Line 4;

```
C     TO USE - - - - - - - - - - -
```

Erase this line.

DATA

At end of each line add the pressure value in atmospheres in the next five spaces with the decimal point in the fifth. Format F5.0.

```
9.289.309.329.339.34STOP
013DES07.948284.800.020000.970
027DES07.948284.800.020005.400
008J   07.500284.700.020000.320
010J   07.840284.400.020000.037
015J   07.990284.700.020000.130
022J   07.970284.700.020000.048
006F   08.100284.800.020000.064
007FSW07.820284.805.400000.057
011F09 07.540284.820.800000.690
017F09 07.540284.827.700000.980
028F   07.360284.731.800000.480
010M   07.650284.733.210000.080
019M   07.230284.833.150000.240
  STOP
```

Figure 3. Format for data presentation (left) to the computer and format of output (below). The data are representative of individual daily measurements taken from a six month experiment in which young trout were first reared in fresh water, which was then gradually changed to sea water during the course of a week or so, and subsequently maintained as sea water.

```
TIME FROM     PH     TEMPERATURE  SALINITY     TOTAL AMMONIA          UNIONIZED AMMONIA
START OF             (K)          (P.P.THOU)  (P.P.M) MICRO G N    (P.P.M)   MICRO G N  PERCENT OF
EXPERIMENT                                            ATOMS/L                ATOMS/L    TOTAL
                                                                                        AMMONIA

013DES        7.948  284.8          0.0200     0.970     69.2      0.017356  1.239      1.78927
027DES        7.948  284.8          0.0200     5.400    385.5      0.096621  6.898      1.78927
008J          7.500  284.7          0.0200     0.320     22.8      0.002049  0.146      0.64045
010J          7.840  284.4          0.0200     0.037      2.6      0.000503  0.036      1.36023
015J          7.990  284.7          0.0200     0.130      9.3      0.002539  0.181      1.95304
022J          7.970  284.7          0.0200     0.048      3.4      0.000896  0.064      1.86679
006F          8.100  284.8          0.0200     0.064      4.6      0.001613  0.115      2.52018
007FSW        7.820  284.8          5.4000     0.057      4.1      DONT EAT THE FISH TODAY
011F09        7.540  284.8         20.8000     0.690     49.3      0.004657  0.332      0.67489
017F09        7.540  284.8         27.7000     0.980     70.0      0.006036  0.431      0.61587
028F          7.360  284.7         31.8000     0.480     34.3      0.001899  0.136      0.39556
010M          7.650  284.7         33.2100     0.080      5.7      0.000615  0.044      0.76840
019M          7.230  284.8         33.1500     0.240     17.1      0.000710  0.051      0.29572
```

Program documentation

he program calculates the fraction of unionized mmonia occurring at the particular condition of H, temperature, salinity and pressure appropriate o each data point in the range encountered in terestrial and ocean water. The unionized ammonia s expressed as

(1) in absolute units, p.p.m.
(2) in absolute units, μg atoms N/1
(3) as a percentage of the total ammonia.

he program is based on the following equations erived from Whitfield's (1974) paper.

reshwater.

$$\begin{aligned}\% \text{ UIA} &= 100\,[1 + \text{antilog}\,(pK_a{}^0\,(\text{T}) - \text{pH}]^{-1}\\ &= 100\,[1 + \text{antilog}\,(18{\cdot}915 - 0{\cdot}0324\\ &\qquad (\text{T} - \text{pH})]^{-1}\end{aligned} \tag{1}$$

ea water.

$$\begin{aligned}\% \text{ UIA} &= 100\,[1 + \text{antilog}\,(pK_a{}^s\,(\text{T})\,(P)\\ &\qquad (I) - \text{pH})]^{-1}\\ &= 100\,[1 + \text{antilog}\,(I + 0{\cdot}0324\\ &\qquad (298 - \text{T}) + 0{\cdot}415\\ &\qquad \left.\frac{P}{\text{T} - \text{pH}}\right)\Bigg]^{-1}\end{aligned} \tag{2}$$

with $I = 19{\cdot}9273\ \text{S}\,(1000 - 1{\cdot}005109\ \text{S})^{-1}$ (3)

and with $pK_a{}^s$ (298°K) (1 atmos) (I) values taken from Whitfield's (1974) full seawater model B, (below), which he recommends.

I molal ionic strength	$pK_a{}^s$ (298°K) (1 atm)	
0·4	9·28 ± 0·01	
0·5	9·30 ± 0·01	
0·6	9·32 ± 0·01	. . . ARRAY
0·7	9·33 ± 0·01	TABLE (I)
0·8	9·34 ± 0·01	

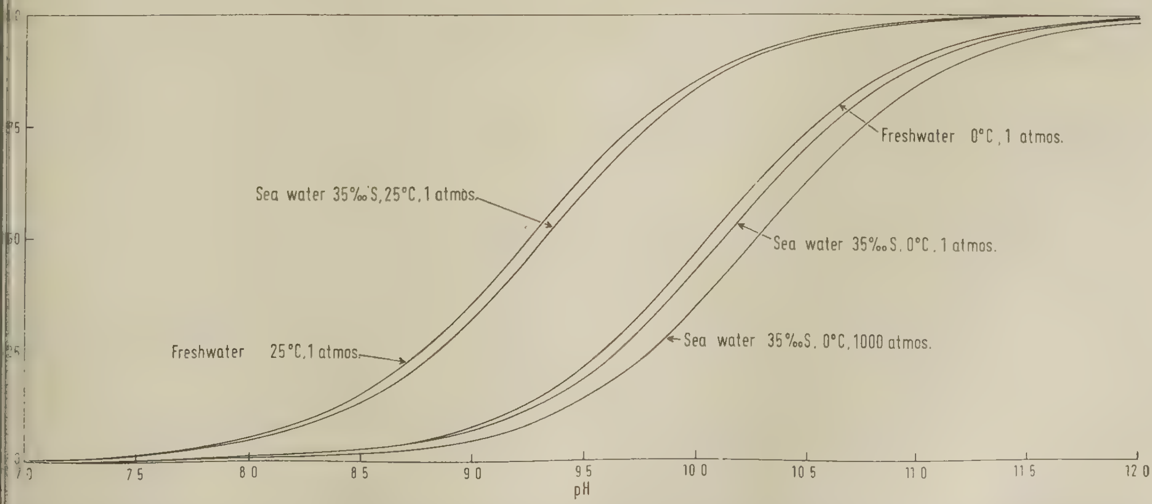
where T = temperature (K)
P = pressure (atm)
S = salinity (‰)
I = ionic strength (M)

$pK_a{}^0$ is the acidic dissociation constant of ammonium ions at 298°K and zero ionic strength.

$pK_a{}^s$ is the stoichiometric acidic hydrolysis constant of ammonium ions in saline water.

The program as listed deals only with ionic strengths at which data for $pK_a{}^s$ are directly available. In other cases error statements are produced; the regression equations dealing with these situations by interpolation are discussed in the appendix to this paper.

The program is written in FORTRAN IV, and is suitable for use with an ICL 1900 computer or with a Hewlett Packard 2100 computer (after slight modification).



igure 4. Typical $pK_a{}^s$ curves (acid dissociation constant for ammonia in saline water) representing the relationship etween percent of unionized ammonia and pH for freshwater and sea water (S 35‰), each at 0°C and at 25°C, and atmosphere pressure. Also $pK_a{}^s$ curve for deep ocean water at 0°C and 1000 atmospheres pressure, corresponding a depth of approximately 10^4m.

Input format

It is essential to adhere to the indicated format (Fig. 3) for data input, i.e. positioning of the data elements, number of significant figures and location of decimal points. The ionic strength array (Fig. 3) occupies the spaces shown on the first line of each batch of data to be processed followed by the characters STOP. The characters STOP occupy the spaces shown after the last line of data. The ranges of the variables are: pH 5 to 12·5, temperature 273° to 308°K, salinity 0 to 40‰ equivalent to ionic strength 0 to 1 M, total ammonia 0 to 99·999 ppm, pressure 1 to 1000 atm.

Unionized ammonia in freshwater, brackish water and sea water

A representation of the way in which the relationship between free ammonia and total ammonia depends on pH, temperature, salinity and pressure for some typical cases spanning the frequently encountered ranges of these variables, as calculated in the above manner, is shown diagramatically on Figure 4.

It may be noted that in the simple case of freshwater some data relating to the percentage of unionized ammonia (UIA) at several levels of pH and temperature have been published by Trussell (1972). These are based on different (and secondary) sources of the dissociation constants of ammonia and water. However, the values of % UIA calculated here and by Trussell are in fair agreement.

Appendix

1. Regression equations to calculate unionized ammonia in brackish water

For the computations of % UIA shown in Figures 3 and 4, the $I/pK_a{}^s$ values from Whitfield's full sea-water model B have been employed (Whitfield, 1974). If one of the alternative models, e.g. model A is preferred, the corresponding values may be substituted on the top line of the data input. In either case values calculated from the respective $I/pK_a{}^s$ regression equations may be used instead of the direct values employed here. Computations of % UIA are then possible in the I (ionic strength) 0·05 to 0·4 region for which data are not available; the values at higher ionic strength are smoothed.

Regression equations:

$$\text{Model B: } pK_a{}^s = 9{\cdot}245 + 0{\cdot}116I$$
$$\text{Model A: } pK_a{}^s = 9{\cdot}245 + 0{\cdot}138I$$

$pK_a{}^s$ in sea water at 25°C and 1 atmosphere pressure

I	0·1	0·2	0·3	0·4	0·5	0·6	0·7	0·8
model B	9·257	9·268	9·280	9·291	9·303	9·315	9·326	9·338
model A	9·259	9·273	9·286	9·300	9·314	9·328	9·342	9·356

(NB These may be listed along the top line of the data input, and a suitable subscript to the array Table viz I, listed).

2. Correct hydrogen ion activities

To ensure correct hydrogen ion activities for th % UIA calculations the pH should be measured or Hansson's sea water pH scales (Hansson, 1973 using the recommended tris-sea water standar buffers of appropriate salinity, and with all measurements and calibrations at the recorded water temperature.

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A study of the response of flatfish (Pleuronectidae) to electrical stimulation

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Direct observations on the reactions of flatfish of the Pleuronectidae to electrical stimulation were made by towing a manned sledge supporting an energised electrode array over the sea bed. The electrical stimulus was pulsed DC, ranging in frequency from 4 to 40 Hz. Involuntary muscular contractions were induced by this stimulus which caused the majority of fish to flee from the electrified zone. Reactions were classified into a few broad categories and the approximate fish size in each observed event was recorded. The results suggested that the most efficient frequency for inducing flatfish to leave the bottom is around 20 Hz, and that large fish are more strongly stimulated by an electric field than small fish; the latter being a significant demonstration under natural conditions of a theory based on aquarium experiments. Observations were made on the reactions of flatfish to a towed chain to assess its comparative efficiency in forcing fish to leave the sea bed.

Introduction

When flatfish of the pleuronectid family are alarmed their first defensive reaction is to burrow into the sea-bed, using a characteristic fluttering movement of their fins to partially cover themselves with mud or sand. Their skin pigmentation is normally adapted to blend with their surroundings, and when motionless and burrowed they are well camouflaged and relatively safe from predators. The author has observed that when threatened by objects being towed over the bottom, flatfish tend not to move until they are in imminent danger of being overrun. They swim rapidly clear of the hazard and immediately reburrow themselves in the bottom. Flatfish gears normally have a chain or rope rigged to scrape along the sea bed and disturb the fish. Some trawls (particularly beam trawls) carry considerable weights of chain requiring powerful and expensive towing vessels. Regular trawling with chains on a fishing ground might have an influence on the bottom fauna; however, there is little evidence available on which to assess the effect of continual "harrowing" of the sea bed.

Aquarium experiments with weak electrical stimulation (low electric field strength DC pulses) demonstrated that flatfish could be induced to flee from electrified zones (Stewart, 1973). This response suggested that an electric stimulus could be used as an aid to capture and might possibly replace the use of chain "ticklers" on trawls. If light weight electric "ticklers" could act as efficiently as heavy chain "ticklers" catch rates with existing gears could be maintained by using smaller, more economical vessels. The experiments described in this paper were carried out to investigate the reactions of flatfish, in their natural environment, to electrical stimulation, with a view to applying the results to the development of improved flatfish gears.

Observations were made by divers from a towed sledge which supported a pulse generating apparatus and an electrode array in contact with the bottom. Reactions to continuously and intermittently pulsed electrical stimulation and to a towed chain were studied. A wide range of pulse frequencies and amplitudes were tested to assess their relative efficiencies in stimulating fish. Observations were made on the reactions of flatfish to a towed chain to assess its comparative efficiency.

An electric field induces muscular contractions. As the frequency of a pulsed electric stimulus is increased, muscle is unable to relax in the interval between pulses and tetanus is induced. The frequency of tetanus for plaice is between 15 and 20 Hz. Clearly a tetanising stimulus will inhibit normal swimming and be inefficient in forcing fish to leave the bottom. An interrupted stimulus will give the fish an opportunity to take evasive action. Initially, therefore, this form of stimulus was used in the experiment, found effective, and studied at length.

The electric field distribution produced by electrodes of a finite size in an unbounded medium like the sea is highly non-uniform, with the zone of high electric field strength concentrated near the electrodes (Stewart, 1975a). Fish distributed randomly in the path of the electrodes will experience electric field strengths within a wide range, and to build up an accurate picture of fish reaction to any given stimulus it was anticipated that a large number of observations would be required. The observations made on responses to a particular stimulating frequency must take account not only of a normal distribution of reaction patterns and intensities, but also of variations due to the range of electric field strengths experienced by the fish. The field strength variation experienced by the fish could be reduced by rigging electrodes at right angles to the direction of motion. Most fish would then experience the maximum available field strength. This would introduce a complication, however, as fish would tend to be herded and their reactions to electrical stimulation would be obscured. For this reason the electrodes were rigged parallel to the direction of motion and in this configuration were found to have no mechanical stimulating effect.

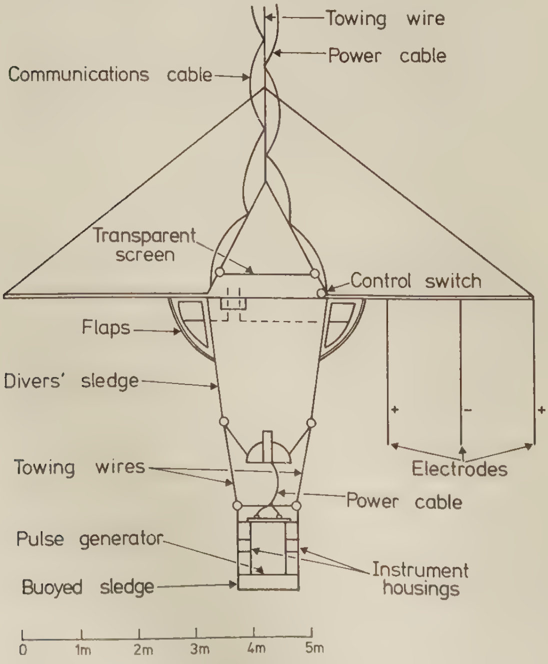

Figure 1. Plan view of towed sledge showing electrode array and pulse generator.

Apparatus and experimental procedures

General

Figure 1 is a schematic diagram of the towed sledge, pulse generator and electrode array. The sledge was towed by a 5 m launch which carried a 3 kW, 50 Hz generator to supply power to the pulse generating apparatus. The pulse generator was mounted on a separate small sledge towed astern of the main sledge. Power was supplied from the surface through a heavy flexible cable lashed to the towing rope and to the underside of the main sledge. The small sledge also carried a number of floats to reduce the weight of the pulse generator, and two small housings which contained equipment for control and monitoring. The electrodes were lengths of 1 cm diameter stainless steel warp, linked together and to the pulse generator output by heavy copper cable. The spar to which they were attached, 1 m apart, was a steel pipe encased in polythene, balanced by an identical spar lashed on the other side of the sledge. The pulse generator was controlled by a switch in a plastic box, mounted at the front of the main sledge. This switch activated a 12 V relay which supplied power to the pulse generator circuit. The circuitry of the pulse generator and the procedure used to handle the apparatus safely under water are described in detail elsewhere (Stewart and Cameron, 1974).

Two divers were required in each experimental tow. One, acting as pilot, operated the flaps and

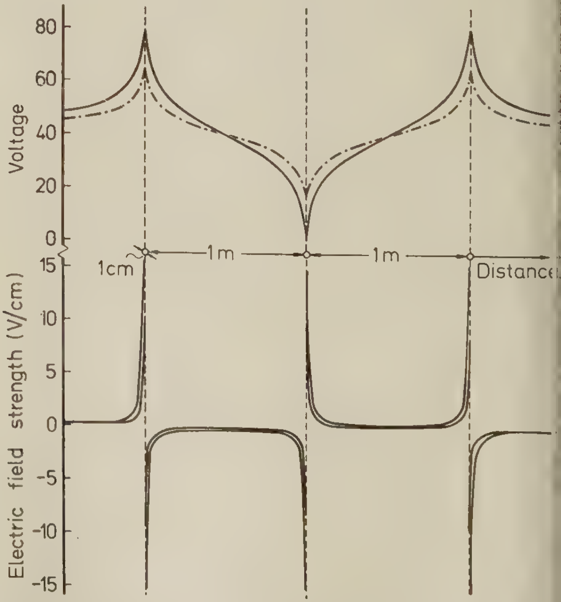

Figure 2. Electric field and voltage distribution between the electrodes.

communicated with the launch coxswain. The other, acting as observer, controlled the supply of energy to the electrodes and continuously recorded descriptions of fish reactions on magnetic tape. The pilot held the sledge a few centimetres off the bottom to give a relatively smooth ride at the towing speeds of 30 to 80 cm s^{-1}.

Electrical stimulus

The stimulus applied to the electrodes was either continuous or 1 second long bursts of exponential shaped DC pulses, with 1 second intervals between bursts, each pulse being of 4 ms duration. The pulse frequencies used were 4, 10, 20, 30 and 40 Hz, and the electrode voltages were normally 50 or 80 V. The voltage and electric field distributions in the plane of the electrodes with these voltages applied are shown in Figure 2. The generator capacity was limited and it was not possible to perform prolonged tests at voltages greater than 50 V at 30 Hz, and 40 V at 40 Hz, without damaging the generator.

Mechanical stimulus

To assess the comparative effect of a mechanical stimulus five tows were carried out with a 1 cm chain. A chain was slung on each side for balance and the

Table 1. Summary of observations of reactions of flatfish to electrical stimulation

Stimulus	Fish size*	Numbers of fish reacting Jump and flight Strong	 Med.	 Weak	 Pulsations	 Paralysis	 Herding	 No reaction	Total no. fish	Total
4 Hz	L	5	4	6	7	–	–	1	23	
50 V	M	2	12	16	20	–	–	–	50	
Continuous	S	8	26	48	48	–	–	–	130	203
4 Hz	L	22	21	11	7	–	1	2	64	
80 V	M	32	41	47	17	–	6	–	143	
1 sec. ON, 1 sec. OFF	S	19	21	67	16	–	–	–	123	330
10 Hz	L	19	24	17	24	–	2	1	87	
50 V	M	15	35	38	27	1	2	2	120	
1 sec. ON, 1 sec. OFF	S	30	59	74	27	–	2	–	192	399
10 Hz	L	2	1	1	4	–	–	–	8	
50 V	M	1	5	3	7	–	–	–	16	
Continuous	S	7	13	14	12	–	2	–	48	72
10 Hz	L	10	10	23	12	–	2	–	57	
80 V	M	27	39	38	26	–	1	–	131	
1 sec. ON, 1 sec. OFF	S	29	37	67	24	–	5	–	162	350
20 Hz	L	32	21	12	15	4	2	–	86	
50 V	M	47	48	29	11	2	4	1	142	
1 sec. ON, 1 sec. OFF	S	47	46	69	4	–	1	–	167	395
20 Hz	L	2	3	–	3	1	–	–	9	
45 V and 65 V	M	3	5	–	1	–	2	–	11	
Continuous	S	14	5	8	6	–	2	–	35	55
20 Hz	L	35	12	6	3	4	3	1	64	
80 V	M	68	49	29	14	8	4	4	176	
1 sec. ON, 1 sec. OFF	S	37	40	31	21	5	–	–	134	374
30 Hz	L	32	12	18	10	17	–	–	89	
50 V	M	58	34	47	13	12	2	–	166	
1 sec. ON, 1 sec. OFF	S	51	43	70	21	2	–	1	188	443
30 Hz	L	4	1	2	1	3	–	–	11	
80 V	M	5	4	5	2	3	–	–	19	
1 sec. ON, 1 sec. OFF	S	8	4	6	–	–	–	–	18	48
40 Hz	L	19	10	6	2	12	–	–	49	
40 V	M	29	28	22	2	15	1	–	97	
1 sec. ON, 1 sec. OFF	S	41	60	49	2	11	–	1	164	310
										2 979

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* Large (L), Medium (M), Small (S).

centres of the chains trailed about 1·3 m behind the spars. The tows lasted 20 to 30 min.

Experimental area

The experiments were carried out in the southern Moray Firth in an area where the bottom is mainly sand, with scattered strips of small stones and weed. The depth in the experimental area ranged between 8 and 12 m. The flat fish seen were mainly plaice *Pleuronectes platessa*, the common dab *Limanda limanda* and the flounder *Platichthys flesus* with a few brill *Scophthalmus rhombus*, lemon sole *Microstomus kitt* and juvenile dover sole *Solea solea*.

Results

General

The observed fish reactions were classified under a few headings to simplify the process of recording underwater. The records for 64 tows are summarized in Tables 1 and 2 for electrical and mechanical stimulation respectively.

The size of each fish observed was recorded on a three point scale; those less than 15 cm being classed as small, 15 to 25 cm as medium, and over 25 cm as large. A simple method of classification was essential so that the divers could record data quickly and accurately. To achieve consistency in reporting, the bulk of the observations were made by two individuals.

Intermittent electrical stimulation

The stimulus was a one second long burst of DC pulses with a one second interval between bursts. The most common reaction produced by this stimulus was a jump off the bottom followed by swimming. The intensity of the reaction was graded on a three point scale; a strong reaction being a violent jump and fast flight; a weak reaction being a small jump and slow movement; and a medium reaction being between the two. Some fish reacted to the field but failed to leave the bottom and swim off. At frequencies below the threshold for tetanus the muscles of these fish reacted to each pulse, giving an effect similar to the normal fin flutter of a flatfish when burying itself. This was described as "pulsations". At frequencies above the threshold for tetanus the muscles were tetanised and the fish arched their backs. This reaction was described as "paralysis". At frequencies close to the threshold for tetanus fish displayed either "paralysis" or "pulsations" according to the field strength which they experienced. A herding reaction was sometimes seen, in which a fish swam either ahead of, or with, the electrodes. Very rarely, no reaction of any kind was noted. It was, however, difficult to see fish which did not move, particularly in conditions of poor visibility. In all, seven types of reaction were recorded.

Fish fleeing from the electrodes nearly always swam to starboard or astern, and rarely swam towards the sledge, suggesting that the electric field was not affecting them enough to cause disorientation or obscure their awareness of other hazards. The 50 V, 4 Hz intermittent stimulus was found to be very weak and observations were made with 50 V, 4 Hz continuous pulsing. To simplify interpretation of the data, the number of fish in each size group observed to react in a certain way has been expressed in Table 3 as a percentage of the total number of fish of that size seen whilst a given stimulus was in use.

Continuous electrical stimulation

The reactions observed depended much more critically than for intermittent stimulation on whether or not the fish were inside or outside the electrified zone. Those within the zone displayed "pulsations" or "paralysis" depending on frequency and voltage. These reactions inhibited swimming and escape until the electrodes had passed over the fish. Most of the strong reactions observed were from fish in front of the electrodes responding strongly on first experiencing the field.

Table 2. Numbers of flatfish reacting to a tickler chain expressed as a percentage of the total number of fish of each size seen to react.

Fish size	Number of fish	Escaped over	Reaction to chain Herded, distance moved 1 m	2 m	3 m	Run over	No reaction
Large	28	67·9	–	21·4	7·1	3·6	–
Medium	64	71·8	7·8	6·3	6·3	7·8	–
Small	52	69·1	5·8	15·4	1·9	3·9	3·9

Table 3. Numbers of flatfish reacting to electrical stimulation expressed as a percentage of the total number of fish of the same size seen with the same stimulus in use.

Stimulus	Fish size*	Percentage of fish reacting							Total no. fish	Total
		Jump and flight			Pulsations	Paralysis	Herding	No reaction		
		Strong	Med.	Weak						
4 Hz	L	21·8	17·4	26·1	30·4	–	–	4·3	23	
50 V	M	4·0	24·0	32·0	40·0	–	–	–	50	
Continuous	S	6·2	20·0	36·9	36·9	–	–	–	130	203
4 Hz	L	34·4	32·8	17·2	10·9	–	1·6	3·1	64	
80 V	M	22·4	28·6	32·9	11·9	–	4·2	–	143	
1 sec. ON, 1 sec. OFF	S	15·5	17·1	54·5	13·0	–	–	–	123	330
10 Hz	L	21·8	27·6	19·5	27·6	–	2·3	1·2	87	
50 V	M	12·5	29·2	31·6	22·5	0·8	1·7	1·7	120	
1 sec. ON, 1 sec. OFF	S	15·6	30·7	38·6	14·1	–	1·0	–	192	399
10 Hz	L	25·0	12·5	12·5	50·0	–	–	–	8	
50 V	M	6·3	31·2	18·7	43·8	–	–	–	16	
Continuous	S	14·6	27·1	29·2	25·0	–	4·1	–	48	72
10 Hz	L	17·5	17·5	40·4	21·1	–	3·5	–	57	
80 V	M	20·6	29·8	29·0	19·8	–	0·8	–	131	
1 sec. ON, 1 sec. OFF	S	17·9	22·8	41·4	14·8	–	3·1	–	162	350
20 Hz	L	37·2	24·4	14·0	17·4	4·7	2·3	–	86	
50 V	M	33·1	33·8	20·4	7·8	1·4	2·8	0·7	142	
1 sec. ON, 1 sec. OFF	S	28·0	28·7	41·3	2·4	–	0·6	–	167	395
20 Hz	L	22·2	33·3	–	33·4	11·1	–	–	9	
45 V and 65 V	M	27·2	45·5	–	9·1	–	18·2	–	11	
Continuous	S	40·0	14·3	22·9	17·1	–	5·7	–	35	55
20 Hz	L	54·7	18·7	9·4	4·7	6·2	4·7	1·6	64	
80 V	M	38·6	27·8	16·5	8·0	4·5	2·3	2·3	176	
1 sec. ON, 1 sec. OFF	S	27·6	29·9	23·1	15·7	3·7	–	–	134	374
30 Hz	L	36·0	13·5	20·2	11·2	19·1	–	–	89	
50 V	M	34·9	20·5	28·3	7·9	7·2	1·2	–	166	
1 sec. ON, 1 sec. OFF	S	27·1	22·9	37·2	11·2	1·1	–	0·5	188	443
30 Hz	L	36·3	9·1	18·2	9·1	27·3	–	–	11	
80 V	M	26·3	21·1	26·3	10·5	15·8	–	–	19	
1 sec. ON, 1 sec. OFF	S	44·4	22·2	33·4	–	–	–	–	18	48
40 Hz	L	38·8	20·4	12·2	4·1	24·5	–	–	49	
40 V	M	29·9	28·9	22·7	2·1	15·4	1·0	–	97	
1 sec. ON, 1 sec. OFF	S	25·0	36·6	29·9	1·2	6·7	–	0·6	164	310
										2 979

* Large (L), Medium (M), Small (S).

Mechanical stimulus

When the 1 cm chain was towed over the bottom the reaction most frequently seen was a quick jump back over the chain (see Table 2). Once over the chain the fish settled on the bottom, and few fish swam as far or as fast as those stimulated by the electric fields. Herding reactions were also seen and are classified according to the distance herded. The chain became clogged with weed and ran over crustaceans and some fish.

The mechanical effect of the electrodes is also of importance and one tow was conducted without an electric field to check on the mechanical tickling effect of the electrodes. Only two fish were observed to move when touched by the electrodes, a significantly lower number of observations than in the electrified tests. On other occasions with the power switched off, the electrodes were seen to touch fish without causing them to move. As far as could be ascertained the electrodes caused negligible damage to the bottom.

Reactions of other species

(i) Roundfish. Most roundfish encountered were small gadoids. On experiencing the field, these displayed either tetanus or pulsations and escaped rapidly in apparently random directions.

(ii) Sandeels (*Ammodytes* spp). The experimental area contained large numbers of this species and an electric stimulus readily forced them out of the bottom. The 40 Hz stimulus induced tetanus which held the sandeels rigid in swimming positions for the 1 second duration of the burst.

(iii) Razor shells (*Ensis* sp). At 30 Hz and above, a prolonged stimulus (eg if the sledge was stationary for electrical tests), induced this species to emerge from the bottom.

(iv) Brown shrimps (*Crangon crangon*). The area was sparsely inhabited by brown shrimps. With the 4 Hz continuous stimulus the jumping behaviour described by de Groot and Boonstra (1970) was observed.

Discussion

Reliability of data

The value of any conclusions drawn from this experiment is dependent on the accuracy with which the divers recorded their observations. Inevitably there will be some variation in classification between individuals, and for each individual on different occasions. There may also have been a tendency to underestimate the number of small fish, as these were difficult to see when their movements were slight, particularly when the visibility was low. An estimate of the accuracy of classification would be useful, and it is possible to obtain comparative data on size classification from catch statistics. In Figure 3 cumulative length distributions for the catches in three hauls carried out in July 1974 in the experimental area are shown. The catch distributions are for the non-electrically stimulated catches recorded during a comparative fishing experiment with a divided gear (Stewart, 1975b).

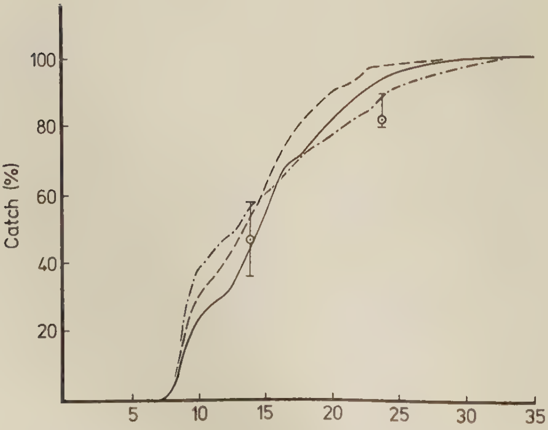

Figure 3. Cumulative fish length distributions for 3 hauls in the experimental area, with divers' size classifications shown.

The divers classified fish below 14 cm as small, 15 to 24 cm as medium and 25 cm and over as large. Summing the observations for each size group in Table 1 shows that 46% of the fish observed were less than 14 cm, and 82% were less than 24 cm. These mean values are shown in Figure 3 with the range covered by the records of all the observers. The divers' size classification is in fair agreement with the catch length distributions suggesting that the data are a reasonable basis for assessing the relative effectiveness of the range of stimuli tested.

Electrical stimulation of flatfish

The experiment has demonstrated that an electrical stimulus is efficient in inducing flatfish to leave the bottom. Both continuous and intermittent stimulalation are effective, but it was considered that the continuous stimulus, which appeared to be more intense, would be less effective if used on a fishing gear. The two reactions produced by the continuous stimulus which make it unsuitable are the rapid flight from in front of the electrodes and the tendency to remain on the bottom, in a state of temporary "shock", after pulsating or being tetanised. The reactions described as "pulsations" and "paralysis" are involuntary but the flight reactions are a response to the disturbing or irritating effect of the electric field. The results show that stimuli with frequencies above the threshold for tetanus (15 to 20 Hz) produced a greater percentage of strong reactions. "Paralysis" was increasingly evident at frequencies of 20 Hz and over, and the incidence of "pulsations" fell as the frequency rose; both results being as expected. Herding reactions were rarely seen, particularly at the higher frequencies. The absence of herding behaviour may be due to there being no part of the electrodes rigged at right angles to the direction of motion. Very few fish failed to react, but since stationary fish were difficult to see, it cannot be concluded that almost every fish reacted. It is possible to draw some conclusions about the relative effectiveness of the various forms of stimulus. The reaction most often seen was a jump followed by swimming. As the frequency is increased there is a trend from a majority of weak reactions to a majority of strong reactions. The greatest percentage of strong reactions was recorded at 20 Hz, 80 V. It is possible that at the higher frequencies the increasing strength of the stimulus, which produces more "paralysis" reactions, tends to inhibit flight in some fish. Comparison of the high and low voltage records for each frequency shows that increasing the voltage tends to increase the percentage of strong reactions. It should be noted that there are limited data for the 30 Hz, 80 V case, and that the 4 Hz, 50 V case, being for a continuous stimulus, includes more strong reactions than would be seen with a 4 Hz, 50 V interrupted stimulus.

The records show that in most cases a greater percentage of large fish exhibited strong reactions than small fish, and that a greater percentage of small fish exhibited weak reactions than large fish. This is the only experimental evidence collected to date by the author which shows a size dependence in the intensity of reaction, and is a significant result as it shows that an electric stimulus can be size selective. For those species of roundfish whose responses to electric fields have been investigated in aquarium conditions it has been found that large fish react at lower field strengths than small fish (Bary, 1956). The reactions of flatfish have not been studied in this way, but there is no reason to suppose that electric fields effect them in a different manner.

The electric field distribution in Figure 2 shows that the high field zone is concentrated close to the electrodes, and the region of maximum intensity is only 30 cm wide. Between each pair of electrodes there is a region 70 cm wide with relatively low and nearly uniform field strength, 30 Vm^{-1} and 18 Vm^{-1} approximately for the 80 V and 50 V cases respectively. Bary (1956) has also reported fish detecting electric field strengths as low as 18 Vm^{-1}. The electric field in the intense zone will be averaged out over the bodies of the fish, thus reducing the apparent peak intensity of the stimulus.

Mechanical stimulation

The reaction of fish to the towed chain was much as expected. It is also efficient in inducing flatfish to leave the bottom although an electric stimulus can induce a more rapid escape reaction.

Applications

The consistency with which fish and shellfish were induced to move by the electric stimulus suggests that it could be useful in surveying areas for flatfish, bottom dwelling shrimps and sandeels. Observations could be made by sonar or underwater TV.

Electric ticklers could be used in place of chain ticklers on trawls to force flatfish off the bottom. De Boer (1969) has measured the drag forces generated by chain ticklers on a beam trawl towed by a 540 h.p. vessel. He found that at maximum towing speed 20% of the total gear resistance was contributed by the friction of the chains on the sea bed. Allowing for vessel drag, the chain resistance was absorbing an estimated 80 h.p. of engine output. To electrify the area covered by the chains on this beam trawl would require a mean power of about 4 h.p., but the surge currents demanded by a large pulse generator might require a source capacity of up to 10 h.p. Replacing chain ticklers by electric ticklers would not necessarily increase the catch-rate, but should permit smaller engined vessels, consuming less fuel, to maintain catch-rates with a given size of gear.

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The fishing power of trawlers in the western English Channel between 1965 and 1968

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Sixty trawlers of over 12·2 m in length landed demersal fish at Brixham, Devon, between 1965 and 1968. Their gross tonnage ranged from 6 to 123 tons, length from 12·2 to 28 m, brake horsepower from 30 to 360 BHP and date of building from 1901 to 1968. During the four year period the average tonnage, length and age of the fleet decreased slightly whereas the average engine power increased from 101 to 147·8 BHP. The fishing power of each vessel was calculated from its catch-rate of total demersal species and of plaice by comparison with a standard group using a modification of Gulland's (1956) method. Significant positive correlations between fishing power and engine power were found. The only other significant correlation was that of total demersal fishing power on tonnage; this was negative and accounted for only 6% of the variance. It was shown that the fishing power of individual vessels varied with time (the average trend was upwards) as a result of a factor (or factors) which had not been included in the analyses. This meant that if the regression equations were used to predict fishing power the result would be biassed. One of the factors responsible was thought to be skipper ability. The published regression coefficients relating fishing power and brake horsepower of motor trawlers in European waters were compared and were found to have a coefficient of variation of 27%.

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Introduction

Since the mid-1950s the English fleet which fishes for demersal species in the western English Channel has undergone major changes affecting both fishing power and the way in which the fleet operates. In the early 1950s a major proportion of the fleet based at the most important port, Brixham, consisted of trawlers 27·4 m in length (90 foot motor fishing vessels (MFVs) built during or just after the 1939–45 War) with a proportion of inshore vessels of less than 12 m. The larger vessels, which were company-owned, operated throughout the English and Bristol Channel making trips of up to 10 days duration; the smaller vessels fished close to Brixham and landed daily. During the late 1950s the number of MFVs operating from Brixham diminished, mainly as a result of the unwillingness of crews to make trips longer than a few days. The increased attractiveness of inshore fishing which followed the introduction of the Decca Navigator System in 1955 also hastened the decline of the MFVs. The MFV crews began to buy their own vessels, which were usually secondhand trawlers of between 12 and 15 m in length, from a number of European countries. By 1965 there were 30 vessels of this type landing at Brixham and only 2 of the old MFVs which were, by now, also skipper-owned. The fleet of vessels in the 12 to 21 m range expanded rapidly after 1965 and reached a peak of 50 vessels in 1968. The increased abundance of a number of species, particularly of plaice and lemon soles, following the cold winter of 1963, contributed to the expansion of the fleet. The expansion was associated with an influx of people from non-fishing families into the industry. During the same period vessels were either re-engined or replaced with new or secondhand vessels of greater engine power. In 1967 an even more significant change began when the first UK-owned double-beam trawler began to operate out of Brixham. Since then twin-beam trawling has been adopted by many fishermen at the port and, in 1975, 19 of the total fleet of 49 vessels used this gear. The period 1965–68, therefore, was a time when otter-trawls were still the predominant gear in use but when changes, such as the replacement of vessels, re-engining and the influx of inexperienced fishermen were probably affecting fishing power.

Gulland (1956) has discussed the causes of differences and changes in the fishing power of a variety of types of fishing vessel and described a technique for calculating the relative fishing power of individual vessels. It depends upon selecting a group of standard vessels whose fishing power is expected to be constant. By estimating the relative density of the fish population from the catch-rates of the standard vessels, the relative fishing power of other vessels, which had fished at the same time and place, may be estimated. Relative fishing power at a particular time is defined by the equation:

$$P_k = d_{kj}/\bar{D}_j \qquad (1)$$

where P_k = fishing power of the kth vessel;
d_{kj} = catch-per-effort of the kth vessel in the jth position;
$\bar{D}_j$ = relative mean density at the jth position according to the standard vessels.

Using the superscript prime (′) to denote that logarithms have been taken, equation (1) becomes:

$$P'_k = d'_{kj} - \bar{D}'_j \qquad (2)$$

The procedure which Gulland advocates is to determine the relationship of fishing power to the characteristics of the ship, such as tonnage, length, engine power or date of building, and to use the relationship to predict the fishing power of other ships at different locations and times using the same gear and fishing for the same types of fish. Other factors, such as skipper ability, although affecting fishing power, were expected to average out so long as they were not correlated with the vessel characteristics being considered.

In principle it should be possible to determine a universal equation for say, otter trawlers fishing for demersal species in European waters, so that a comparable measure of effective fishing effort could be determined for any time or location. The advantages of having such a measure so that comparisons of relative density can be made in time and space, are obvious. However, in the 20 years since Gulland's work, such a measure has not appeared. The need for estimates of relative density has not been crucial to stock assessments in the Northeast Atlantic area, principally because so called "unit stocks" have been the units of management and the virtual population technique has been found adequate for estimating fishing mortality. Should it become necessary to manage fish populations in units less than stock level by, for example, setting restrictions on fishing differentially for different parts of a stock, then the need for estimates of relative density will become crucial both for modelling the distribution of fish within the stock boundary and for interpreting the results of fish tagging experiments.

The present paper examines the relationship of fishing power to the vessel characteristics of trawlers landing at Brixham between 1965 and 1968. The results are compared with similar analyses of the determinants of fishing power, and the feasibility of achieving a generally applicable model for predicting fishing power is discussed.

Methods

The method used for calculating fishing power follows Gulland (1956) in principle. The analysis was carried out on the catch-rates of all motor trawlers over 12·18 m (40 feet) in length which landed at Brixham from the ICES standard statistical rectangle E629 (50°N to 50°30′N; 3°W to 4°W) in the period 1965–68. The catch-rate of total demersal species and of plaice (*Pleuronectes platessa*) of each vessel was determined for each month in which fishing took place. The source of these data was the Ministry of Agriculture, Fisheries & Food (MAFF) F-form system in which the catch, effort and rectangle at capture of each landing or group of landings by individual vessels are recorded.

From the fleet a group of standard vessels was selected, whose characteristics (principally engine power) were thought not to have changed during the period and which had fished rectangle E629 during as great a number of months as possible during the 4 years. The vessel characteristics of these and the remaining vessels were obtained from a variety of sources including Board of Trade records, MAFF records, the White Fish Authority, skippers, owners and others. No single source could provide the engine power information with sufficient accuracy and a considerable amount of cross-checking was necessary to obtain a consistent list of characteristics. Particular attention was paid to the dates when engines were replaced in particular vessels. Brake horsepower (BHP) was adopted as standard as were gross tonnage (GT) and length between perpendiculars (L.).* These are not ideal for a functional analysis of fishing power but are the most easily available, and therefore practical, measures. Date of building of the vessel was also considered. BHP, GT and L were obtained for each of the 68 vessels which landed during the period. Ten vessels were found to have been re-engined and the date of building was available for 60 vessels.

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* GT and L were obtained from the vessels' certificates of registration. GT is calculated from the formula $GT = L \times B \times D \times O \cdot 45/100$ where B is breadth, D is depth and L is the length between perpendiculars (in feet).

The fishing power of the ith standard vessel ($i = 1, n$) relative to the other vessels in the standard group ($l = 1, n - 1$) was calculated over the m months ($j = 1, m$) when they all fished together:

$$P'_i = \frac{1}{n-1} \Sigma_l \frac{1}{m} \Sigma_j (d'_{ij} - d'_{lj}) \qquad (3)$$

where P'_i is the log fishing power of the ith standard vessel and d'_{ij} (d'_{lj}) is the log catch per unit effort of the ith (lth) standard vessel in the jth month. The relative mean density in each month was then determined from the catch-rates of the standard vessels which fished in the month and their relative fishing powers:

$$D'_j = \frac{1}{n} \Sigma_i (d'_{ij} - P'_i) \qquad (4)$$

where D'_j is the log mean density in the jth month and n is the number of standard vessels which fished. From this estimated density the fishing power of the kth non-standard vessel was calculated over the m months ($j = 1, m$) in which it fished:

$$P'_k = \frac{1}{m} \Sigma_j (d'_{kj} - D'_j) \qquad (5)$$

The estimated fishing power of a non-standard vessel is, therefore, an average based upon a series of monthly estimates. These calculations were carried out using the catch-rates of all demersal species combined and also of plaice in rectangle E629. Logarithms to base 10 have been used throughout this paper.

The effect of vessel characteristics on both total demersal and plaice fishing power was tested by subjecting the data to multiple correlation analysis. The trend in the mean deviation of monthly fishing power from the average has been used to provide additional information on the suitability of the regression models for estimating effective fishing effort.

Results

Vessel characteristics

Table 1 is a summary of the composition of the fleet at Brixham between 1965 and 1968. The majority of vessels were in the range 10 to 29 tons and 12 to 15 m. There was relatively greater variation in BHP and in date of building than in GT or L. The mean value of each characteristic for each year is given in Table 2. Whereas both GT and L decreased slightly between 1965 and 1968, engine power increased from 101 to 147·8 BHP. The average age of the vessels decreased from 24·3 years to 21·1 years.

Simple correlation coefficients between the 4 vessel characteristics for 70 fishing units (60 plus 10 re-engined) are shown in Table 3. As might be expected significant positive correlations were found between GT, L and BHP. In addition the table shows that the younger vessels had more powerful engines than older ones. The tendency for younger vessels to be smaller was not significant.

The 8 standard vessels selected from the fleet had fished throughout the 4-year period and had not been re-engined. The GT of the standard group ranged from 12 to 24 and averaged 16·9; L ranged from 12·2 to 14·6 m and averaged 13·2; BHP ranged

Table 1. Vessel characteristics of trawlers which landed at Brixham between 1965 and 1968 from ICES rectangle E629, showing the number of vessels (n) in each class interval for gross tonnage (GT), length (L in metres), brake horsepower (BHP) and date of building (DB).

Gross tonnage		Length		BHP		Date of Building	
GT Class	*n*	L Class	*n*	BHP Class	*n*	DB Class	*n*
0– 9	1	12–13	37	0– 49	5	1900–4	1
10– 19	29	14–15	12	50– 99	24	1905–9	–
20– 29	23	16–17	6	100–149	15 (2)	1910–4	1
30– 39	3	18–19	6	150–199	14 (3)	1915–9	1
40– 49	6	20–21	4	200–249	7 (2)	1920–4	1
50– 59	2	22–23	1	250–299	1 (3)	1925–9	5
60– 69	1	24–25	–	300–349	1	1930–4	4
70– 79	–	26–27	–	350–399	1	1935–9	4
80– 89	1	28–29	2			1940–4	10
90– 99	–					1945–9	13
100–109	–					1950–4	3
110–119	1					1955–9	6
120–129	1					1960–4	4
						1965–8	7
						?	8
Totals	68		68		68 (10)		68

Table 2. Average vessel characteristics of the trawler fleet at Brixham in the years 1965 to 1968 and the number of different vessels which fished. (abbreviations as in Table 1).

Year	1965	1966	1967	1968
Mean GT............	28·6	25·5	26·9	24·8
Mean L..............	15·1	14·9	15·1	14·7
Mean BHP..........	101·0	103·5	131·9	147·8
Mean DB............	1941·2	1942·6	1945·0	1947·4
Vessels..............	30	38	44	50

Table 3. Simple correlation coefficients (r) between vessel characteristics calculated for the 70 units for which information was available. (abbreviations as in Table 1).

	GT	L	BHP	DB
GT.......	1·000	0·934**	0·673**	−0·003
L.........		1·000	0·667**	−0·060
BHP......			1·000	0·2776*
DB.......				1·000

* $P < 0{\cdot}05$ ** $P < 0{\cdot}01$

from 30 to 124 and averaged 82·9; date of building ranged from 1914 to 1960 and averaged 1942·7.

Fishing power

The distribution of log catch per unit effort (total demersal) of the 8 standard vessels in the 23 months in which they fished together was found to be normally distributed (chi-squared = 6·13 for 6 degrees of freedom). Table 4 presents the results of an analysis of variance on these data. There were significant differences in catch-rates between months and between vessels. The residual variance is small and it is therefore a reasonable procedure to use the log catch per unit effort to estimate the relative fishing power of each standard vessel. A similar result was obtained when plaice catch-rates were used in the analysis.

The fishing power of each standard vessel relative to the other 7 in the group, the relative mean density in each month and the fishing power of each non-standard vessel, were calculated using Equations (3), (4) and (5) from total demersal catch-rates and plaice catch-rates separately. In Figure 1 log plaice fishing power has been plotted against log total demersal fishing power for each fishing unit, except two which did not catch plaice. The two parameters are positively correlated ($r = 0{\cdot}54$ for the 74 degrees of freedom). This is not surprising since plaice form part of the total demersal catch and therefore the parameters are not independent. However the graph does show that the correlation is far from perfect and that, in some cases, a good plaice catching vessel can be a poor all-rounder and vice-versa.

Table 4. Analysis of variance on log total demersal catch per 100 hours fishing of the standard vessels.

Source of variation	Sums of squares	Degrees of freedom	Mean square	Variance ratio	P
Months .	0·9342	22	0·0425	3·26	0·01**
Vessels . .	0·8771	7	0·1253	9·62	0·01**
Residual	2·0059	154	0·0130		
Total . . .	3·8172	183			

The deviation of each monthly estimate of fishing power from the vessel average was found for each vessel. A simple numerical example (not given here) is sufficient to show that the mean monthly deviation of the fishing power of the standard vessels is always zero even though, individually, the standard vessels

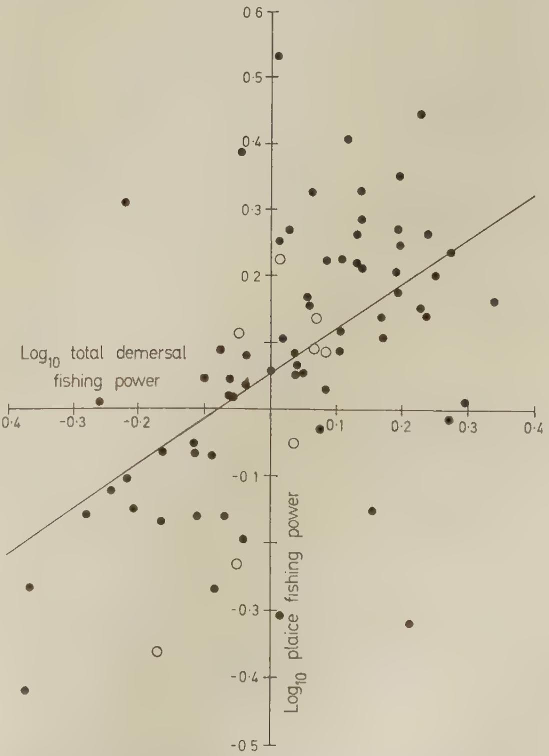

Figure 1. Relationship between plaice fishing power and total demersal fishing power (in logs) for 76 fishing units which landed at Brixham from rectangle E629 between 1965 and 1968. ($r = 0{\cdot}54$ for 74 degrees of freedom). The standard vessels are shown with an open circle.

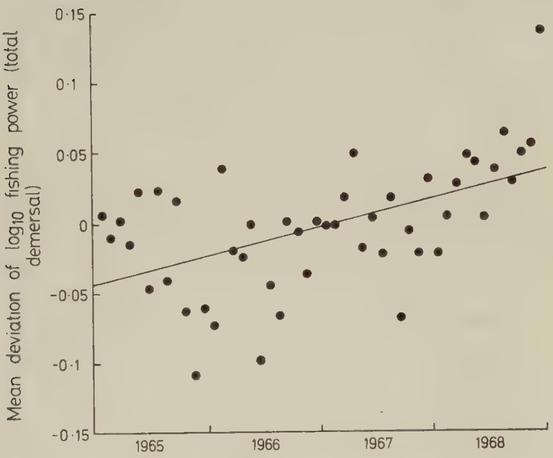

Figure 2. Plot of the mean monthly deviation of fishing power from the individual vessel average against date for the Brixham fleet and calculated regression line. ($r = 0{\cdot}51$ for 46 degrees of freedom).

may show either no trend, an upward trend or a downward trend in fishing power with time. The results confirmed that this was so. The mean deviation of the non-standard vessels is not pre-determined and may show considerable variation. In Figure 2 the mean monthly deviation of total demersal fishing power of the entire fleet has been plotted against time. This shows a significant positive trend ($r = 0{\cdot}51$ for 46 degrees of freedom) corresponding to a 20·1% increase in fishing power relative to the standard vessels, over the 4 year period. The relevance of this result will be dealt with in the discussion.

Dependence of fishing power on vessel characteristics

Multiple correlation analysis was carried out to test the hypothesis that there was no effect of the 4 vessel characteristics on fishing power. The analysis was carried out initially on both linear and logarithmically transformed data. The log transformation resulted in a lower correlation for total demersal fishing power and a slightly higher correlation for plaice fishing power. This suggests that the latter relationship is a power function. For simplicity only the results of the linear analyses are shown in Table 5. All 6 variables were available for only 68 of the 78 fishing units which landed during the period and so the analyses were restricted to these 68.

Both of the regressions are highly significant showing that there was an effect of the vessel characteristics on fishing power. In the regression of total demersal fishing power, 66·5% of the variance is accounted for by the regression equation, whereas only 21·5% of the variance of plaice fishing power is accounted for by the second regression. The partial correlation coefficients show that when the effect of brake horsepower is removed the correlations became less significant. There is, however, a significant negative correlation of gross tonnage on total demersal fishing power. Brake horsepower certainly has the greatest effect on fishing power and the relationships are almost as well represented by regressions of fishing power on this vessel characteristic alone, as shown at the bottom of Table 5.

Table 5. Multiple and partial correlation coefficients (r) between fishing power (y) and date of building (1), gross tònnage (2), length in metres (3) and brake horsepower (4), for trawlers landing at Brixham from rectangle E629 between 1965 and 1968.
(Equation: $y = b_1 \cdot \mathrm{DB} + b_2 \cdot \mathrm{GT} + b_3 \cdot \mathrm{L} + b_4 \cdot \mathrm{BHP} + c$). Also included are the regression and correlation coefficients between fishing power and brake horsepower alone (Equation: $y = b \cdot \mathrm{BHP} + c$).

y	Total demersal fishing power	Plaice fishing power
n	68	68
r_{y1234}	0·82**	0·46**
$r_{y1.234}$	−0·15	0·12
$r_{y2.134}$	−0·24*	−0·07
$r_{y3.124}$	0·03	0·04
$r_{y4.123}$	0·77**	0·33**
b_1	−0·0029	0·0054
b_2	−0·0075	−0·0050
b_3	0·0005	0·0015
b_4	0·0054	0·0036
c	0·6429	0·4571
r_{y4}	0·77**	0·44**
b	0·0040	0·0034
c	0·5808	0·8292

* $P < 0{\cdot}05$ ** $P < 0{\cdot}01$

Discussion

The principal aim of this study was to obtain a regression equation which could be used to estimate the effective fishing effort in the Brixham fishery for years other than 1965 to 1968 using vessel characteristics (effective effort is defined as actual effort multiplied by fishing power). In this study, and in a number of other studies (Gulland, 1956; Zijlstra and de Veen, 1963; Hovart and Michielsen, 1975; Guichet, 1975) significant relationships between fishing power and vessel characteristics have been found. The extent to which these relationships can be applied elsewhere and at other times is dependent upon whether they include all the main determinants of fishing power as independent variables. The results of the Brixham analysis indicate that this condition has not been fulfilled in the present study.

It was shown that, relative to the standard vessels, the Brixham fleet exhibited an upward trend in the mean deviation of fishing power from the individual averages during the period 1965 to 1968. Individually the vessels showed either no trend, an upward or a downward trend in fishing power. The mere existence of the trends indicates that one or more time-dependent factors influenced the fishing power of individual vessels at Brixham. The absolute sign and value of the trends is uncertain since they have been estimated relative to a group of standard vessels which also exhibited individual trends in fishing power and which, consequently, cannot rightly be assumed to have had a constant fishing power over the 1965 to 1968 period. The result of this is that the application of the regression equation to estimate the effective effort of the fleet either outside or even within the study period will lead to estimates which are potentially biased.

As an example, if one could assume that the fishing power of the standard vessels did not change between 1965 and 1968, then the regression (which predicts the average fishing power of a vessel over the 4 years) would over-estimate the fishing power of the fleet at the beginning of the period and under-estimate it at the end, because, as has been shown, the fleet exhibits an upward trend in the mean deviation of fishing power relative to the standard vessels. The estimates of effective fishing effort obtained by using the regression equation would be similarly biased; in fact the difference between the effective effort estimated from the standard vessels and that estimated from the regression was found to be 20% over the 4-year period. The potential magnitude of the bias is at least as great as this and could be more, if, in reality, the standard vessels possessed a downward trend in fishing power.

The main point is that unless the regression equation includes all the main determinants of fishing power, then the application of it to fisheries at different times or locations is probably invalid. The danger of the regression technique as such is that, once a relationship is found, then this may be (erroneously) regarded as a complete predictive model.

As to the cause of the trends in fishing power, these must be determined by factors which cause changes in the fishing power of individual vessels rather than factors which cause only differences between vessels. Fixed characteristics such as tonnage and length are therefore ruled out.

Conceivably the increasing age of individual vessels could cause trends in fishing power (albeit mainly downward) but, if this were the case, the effect of date of building on fishing power should have been statistically significant in the regression analysis and it was not. Changes in realizable engine power would be related to increased age and can be discounted for similar reasons. The causes of individual trends in fishing power must therefore be factors which have not been considered in the analysis. The most likely factors are changes in gear efficiency and the ability of skippers. The principal gear in use at Brixham in 1965 to 1968 was a local design called the "Brixham slack-back trawl" and to my knowledge this had been in use for a number of years at the port and there was no tendency to adopt different patterns or rigs during the period 1965–68. As has been pointed out, the period 1965 to 1968 was a time when people inexperienced in fishing were entering the fishery, but, unfortunately, it has not been possible to quantify this change. The crews of the standard vessels might have been stable in this respect and so a general upward trend in fishing power of the remainder of the fleet could be attributed to improvements in skipper ability. Gulland (1956) has suggested that the effect of this factor on fishing power would tend to even out in time. This is probably true but, if the above interpretation of the trends is correct, the time scale of the levelling out process is longer than 4 years, and so for some applications (estimating mortalities for instance) this factor should be included in the regression model.

The feasibility of constructing a generally applicable regression model for predicting fishing power is thus dependent upon including within it all factors which could conceivably affect fishing power. Irrespective of whether comparisons are to be made in either time or space or in both, it is appropriate to consider, at least, tonnage, engine power, date of building, skipper ability and general differences in the gear. The inclusion of gears which have different selective actions (inter- or intra-specific) is probably inappropriate although the model could include, say beam and otter trawls if the general difference in efficiency were accounted for. Scaling factors between different otter trawl rigs, such as the presence or absence of tickler chains, would also have to be included for the model to be generally useful.

Table 6 is a summary of all the regression coefficients between fishing power and brake horsepower for motor trawlers in European waters which have so far been published including those from the present study. Both otter and beam trawls are included and undoubtedly the data refer to a variety of otter-trawl rigs and different object species. The final column, calculated from the regressions, is the

Table 6. Summary of the published regression coefficients for the relationship between fishing power (P) and horsepower (BHP) of motor trawlers fishing for demersal species in European waters (Equation: $P = b \cdot \text{BHP} + c$). a. Gulland (1956); b. Zijlstra and de Veen (1963); c. Hovart and Michielsen (1975); d. Guichet (1975); e. This paper. The final column is the fishing power per unit BHP relative to the fishing power of a 200 BHP vessel

Author	Gear	Species	BHP range	b	c	P/BHP
a.	Otter	All demersal	150–400	0·0055	1·22	0·00237
b.	Otter	Plaice	100–480	0·0059	0·51	0·00349
b.	Otter	Sole	100–480	0·0040	0·29	0·00367
c.	Beam	Mainly sole	130–480	0·00612	1·186	0·00254
c.	Beam	Mainly sole	145–480	0·00493	1·188	0·00226
c.	Beam	Mainly sole	130–450	0·00640	0·890	0·00295
d.	Otter	Hake	200–350	0·00089	0·189	0·00243
d.	Otter	Hake	500–800	0·00067	0·431	0·00119
e.	Otter	All demersal	30–360	0·0040	0·581	0·00290
e.	Otter	Plaice	30–360	0·0034	0·829	0·00225

fishing power per unit brake horsepower relative to a 200 BHP vessel as standard. The average value of this parameter is $2{\cdot}605 \times 10^{-3}$ with a standard deviation of $7{\cdot}04 \times 10^{-4}$ and a coefficient of variation of 27%. It is encouraging that such a consistent effect of brake horsepower on fishing power exists for such a variety of vessels, gears and object species. Although engine power is only one of the determinants of fishing power the close agreement is a pointer to the feasibility of constructing a generally applicable regression model of fishing power.

Summary

1. Changes in the trawler fleet at Brixham, Devon between 1950 and 1975 are discussed and the composition of the fleet in terms of tonnage, length, engine power and age in the period 1965–68 are described in detail.
2. The relative fishing power of each trawler landing at Brixham between 1965 and 1968 was calculated from total demersal catches and plaice catches using a method based upon Gulland (1956).
3. The dependence of fishing power on tonnage, length, brake horsepower and date of building was tested using multiple correlation analysis. Brake horsepower had the greatest effect and when its effect was removed the only significant correlation remaining was that of tonnage on total demersal fishing power and this was negative.
4. The regressions were shown to be unsuitable for estimating effective fishing effort even in the study situation. The reason put forward to explain this was that another factor, not considered in the regressions, had an effect on fishing power and this factor was likely to be skipper ability.
5. The feasibility of constructing a generally applicable regression model was discussed and it was shown that relationships between fishing power and brake horsepower for a variety of trawl gears, vessels and object species showed good agreement supporting the view that such a model is feasible.

Acknowledgements

My thanks are due to numerous colleagues who assisted with the tedious process of data extraction, to Mr Alec Sharples of the White Fish Authority, Plymouth who supplied information on dates of re-engining and to the good memory of Mr Frank Bowles, marine engineer of Brixham, who helped to compile the list of vessel characteristics. I would also like to pay tribute to Lionel Ross who collected the catch and effort data.

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The problem of the salinity increase in Lake Qarun (Egypt) and a proposed solution

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Lake Qarun, which was once a fresh water body, is now a saline closed basin and is used as a reservoir for drainage water of the surrounding cultivated lands. A certain amount of salt is carried annually to the lake by drainage water and causes the salt content and the salinity of the lake to increase with time. The salt content increased from 11×10^9 kg in 1906 to 33×10^9 kg in 1970 and the salinity rose from 11 ‰ to 31·7 ‰ in the same period. At present, the rate of salinity increase is estimated as 0·35 ‰ per year with the water level of the lake controlled at a constant value. The forecasted salinities in the next 75 years are given from which it is concluded that the salinity might be over 60 ‰ at the end of this period if nothing is done to change the present trend. The lake is expected to be a "dead" water body if the salinity continues to increase at its present rate. Two proposals are given for complete control of the salinity of the lake. By the first, the salinity would increase slowly and reach an equilibrium value of 41 ‰ while by the other, the salinity assymptotically approaches the equilibrium value of 12·4 ‰.

Introduction

Lake Qarun is an inland closed basin of about 40 km length, 5·7 km mean breadth and 4·2 m mean depth. It is situated in Faiyum, a province in Middle Egypt (Fig. 1). The lake occupies the deepest part of the Faiyum Depression which is an isolated basin lying in the Western Desert about 100 km south west of Cairo. The lake is surrounded by cultivated lands from its southern and south eastern sides which slope with steep inclination towards the lake. This provides a natural aid for using the lake as a sink for drainage water of the cultivated lands of the whole province of Faiyum. The water level of Lake Qarum lies below mean sea level and is controlled by the inflow of drainage water and by evaporation which represents the only outflow. The area and volume of Lake Quarum vary with the variation of its water level. In 1970, the water level was fluctuating around −43·9 m at which level the lake covers an area of 240·6 km² and has a corresponding volume of 1·05 km³.

At present Lake Qarun is faced with two main problems, namely: the progressive increase of its salinity with time and the need for lowering its water level. This is a delicate balance because, if the volume of drainage water exceeds evaporation, the water level of the lake will rise and may flood the neighbouring cultivated and inhabited areas since the capacity of the lake is limited. On the other hand, if the opposite occurs, the salinity of the water will increase. Since the drainage water represents about 20% of the total supply of irrigation water to Faiyum Province, it follows that the cultivated area in Faiyum is tightly controlled by the water level of Lake Quarun. Expansion of the existing lands means consumption of more irrigation water and hence conveying additional inflow of drainage water to the lake.

The average salinity was estimated in 1970 as 31·73 ‰ and it varies from season to season according to the fluctuations in its water level. The salinity of the lake tends to undergo progressive increase with time. This is due to the fact that the lake receives an annual volume of drainage water in the order of 350×10^6 m³ which has an average salt content of 1·1 ‰ (Meshal, 1973). It follows that an average of about 385×10^6 kg of salts, which are washed out annually from the cultivated lands, are conveyed to the lake. In the same time, a volume of freshwater, nearly equal to that of the inflowing drainage water

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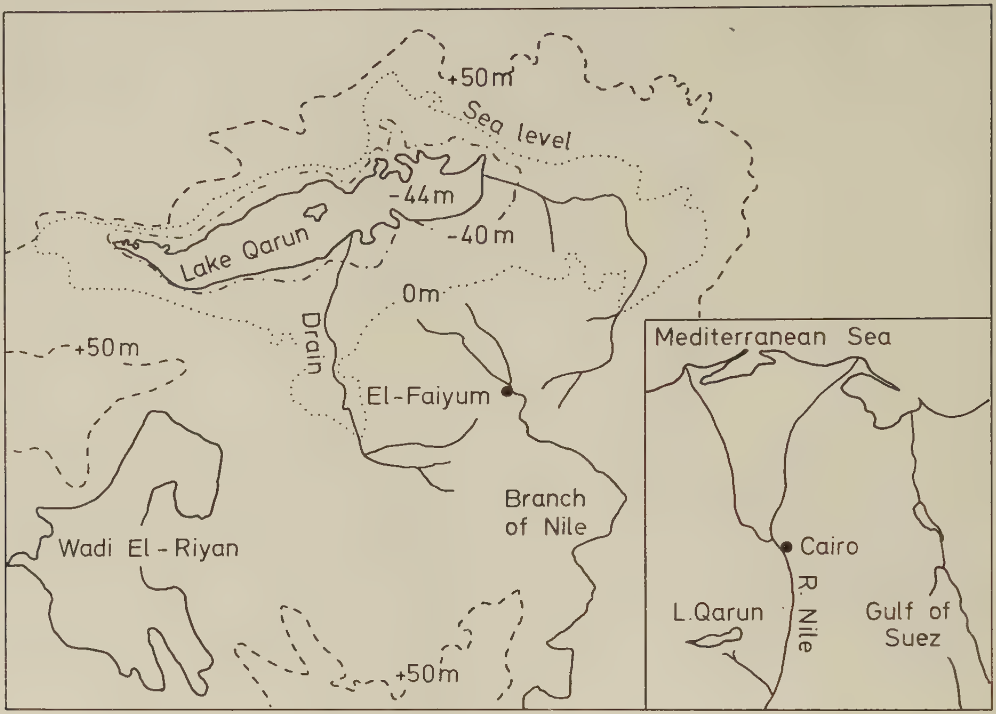

Figure 1. Location of Lake Qarun in Faiyum Province showing the slope of the surrounding land towards the lake.

is lost annually from the lake through evaporation while the dissolved salts are left in the lake. Consequently, the salt content increases and if the volume of the lake remains constant, the salinity will continously increase. This continuous increase in salinity is the major problem facing the lake and threatening its fisheries in the future.

The investigation of the rate of increase of salinity of Lake Qarun requires a review of its history and a tracing of the early observations of salinity which were made and recorded in the literature.

Historical review of lake Qarun

Lake Qarun is the remanent of a natural freshwater reservoir which existed in Faiyum from prehistoric times filling the entire Faiyum Depression to a level of about 25 m above the sea level (Ball, 1939). That natural reservoir then became artificially controlled by ancient Egyptians of the Twelfth Dynasty who constructed a dam across the channel of communication with the River Nile. This formed what was known as Lake Moeris which has been used to receive inflow from the Nile during the annual flood and to supply the Nile Valley with water during the drought period (Caton-Thomson and Gardiner, 1929). Lake Moeris then became disconnected from the Nile and evaporation might have caused its water surface to drop to lower levels leaving large areas of land for cultivation. Drainage water from these lands was directed to flow into Lake Moeris. The existing saline Lake Qarun is the remanent of the shrunken and once fresh water Lake Moeris.

Salinity increase in the period from 1901 to 1970

The earliest observation of the "salinity" of the water of Lake Qarun was made in March 1901 when a single water sample was collected from its western part (Lucas, 1906). Later in December 1905 two water samples were collected by the Survey Department of Egypt near El-Qarn Island. In February 1906 the Survey Department collected water samples at five stations in the central part of the lake at the surface and bottom. In the same year 36 surface water samples were collected from positions well distributed in the lake. The sampling process appears to have been stopped until 1918 when the Coast Guard Administration started a regular sampling from six stations during the four seasons of the year up to 1932 (Ball, 1939). Fouad (1928) gave an outline of the "salinity" of the lake in the period from 1921 to 1926. In all these observations, the "salinity" was considered as the total dissolved salts expressed in grams per litre (g/l) (Lucas, 1906; Fouad, 1928; Azidiam and Hug, 1929; and Ball, 1939).

Naguib (1958) studied the salinity of Lake Qarun by collecting water samples from 13 stations during the period from November 1953 to February 1955 inclusive. He estimated the salinity by determining chlorinity and using Knudsen's Hydrographical Tables (Knudsen, 1901).

The author carried out monthly investigation of salinity in the lake during the period from January 1970 to March 1971. Twenty-two hydrographic stations, well distributed in the lake and representing its different regions, were occupied regularly every month where water samples were obtained at the surface, 0·5, 2, 4 and 6 m or as many of these levels as allowed by the depth of water at each station. The electrical conductivity of the water samples was measured and converted to salinity by the use of an empirical relationship established for Lake Qarun (Meshal, 1973).

The determination of salinity by different methods makes a comparative study between the older data and the relatively recent observations difficult. Determining the salinity as the total salts gives erroneous results since the salinity by its definition (Forch, Knudsen and Sorensen, 1902) is less than the total salt content (Harvey, 1957). Similarly, the application to Lake Qarun of the Knudsen equation proposed for sea water requires that the relative proportions of the major constituents be identical in both sea and lake waters. This requirement is not met since there is an appreciable difference between their relative composition. Bearing that in mind, the author established an empirical equation relating chlorinity and electrical conductivity with salinity as determined by the direct gravimetric method (Meshal, 1973). It was concluded that the use of the Knudsen equation for Lake Qarun gives salinity values which are on the average 72·6% of the value of salinity as determined gravimetrically. The 1970 salinity values were estimated on this basis and are considered here as the virtual salinity of the lake. Hence, it was decided to recalculate the older "salinity" data in order to be more consistent and comparable with that of 1970 as follows:

1) For the period from 1901 to 1932, the total salt content (in g/l) is divided by the corresponding density to change its unit to g/kg, which in turn is converted to salinity (‰) using a reduction factor of 0·25% (inferred from Harvey, 1957, Table 1, p. 4) i.e.:

$$\text{Salinity ‰} = \frac{\text{total salt (g/l)}}{\text{density}} \times 0{\cdot}997$$

2) The 1953–1955 salinity values were raised by 37·7% (Meshal, 1973).

Table 1 lists all the recorded salinity observations in Lake Qarun for a period of seventy years (1901–1970) arranged in chronological order after re-

Table 1. Summary of the observations of the total salts (g/l) and the corrected salinity (‰) of Lake Qarun which were made from 1901 to 1970

Year	Water level (m)	No. of samples	No. of stations	Location of stations	Total salts g/l	Corrected salinity ‰	Reference
1901	−44·90	1	1	Extreme western part	13·42	13·25	Lucas (1906)
1905	−44·62	2	2	Near El-Qarn Island	8·56	8·50	Lucas (1906)
1906	−44·30	46	36		11·06	10·96	Lucas (1906)
1918	−44·63	6	6		18·0	17·7	Ball (1939)
1919	−44·86	6	6		18·4	18·1	Ball (1939)
1920	−44·62	6	6		17·6	17·4	Ball (1939)
1921	−45·00	6	6		19·2	18·9	Azidian and Hug (1929)
1922	−45·25	6	6	Well distributed in the northern, southern and central parts of the lake	21·6	21·2	Azidian and Hug (1929)
1925	−45·10	6	6		23·4	23·0	Azidian and Hug (1929)
1926	−44·99	6	6		22·4	22·0	Azidian and Hug (1929)
1927	−44·95	6	6		22·3	21·9	Azidian and Hug (1929)
1928	−45·10	6	6		24·3	23·8	Azidian and Hug (1929)
1929	−45·23	6	6		24·7	24·2	Ball (1939)
1930	−45·15	6	6		23·6	23·2	Ball (1939)
1931	−45·37	6	6		27·4	26·8	Ball (1939)
1932	−45·77	6	6		31·6	30·8	Ball (1939)
1954	−44·92	400	11		–	31·49	Naguib (1958)
1970	−43·89	600	20		–	31·73	Meshal (1973)

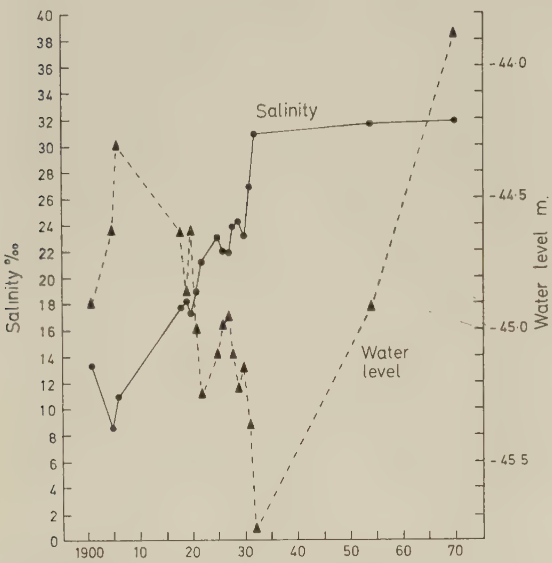

Figure 2. Variation of the average salinity and water level of Lake Qarun from 1901 to 1970.

calculating the salinity as described above. It is noticed that the average salinity in 1901 was appreciably higher than the 1905 and 1906 values. This is attributed to the fact that the 1901 sample was obtained from the western end of the lake where the salinity is maximum while the 1905 and 1906 samples were collected near the inlet of the main drain and in the central part of the lake respectively. In addition, the water level of the lake in 1901 was much lower than that in 1905 which in turn was lower than the 1906 level (Fig. 2). Similarly, the drop in salinity values in 1920, 1926, 1927 and 1930 could have resulted from an increase in the water level and hence in the volume of water contained in the lake. By the same reasoning we can explain why the average salinity did not show an appreciable increase in the periods from 1932 to 1954 (0·03 ‰ per year) and from 1954 to 1970 (0·015 ‰ per year). Figure 2 shows that the salinity variation is roughly a mirror image of the fluctuation in the water level. Any drop in salinity was accompanied by a simultaneous rise in the water level. It is understood that the increase in the water level of Lake Qarun is caused by the excess of drainage water (S = 1 ‰) over evaporation resulting in diluting the lake water.

However, a better picture of the progressive increase of salinity is obtained when long term variations are considered. Thus, the annual increase was 0·5 ‰ during the period from 1906 to 1920; 0·6 ‰ from 1920 to 1930 and 0·2 ‰ from 1930 to 1970. Again the rate of increase fluctuates according to the variation of the water level of Lake Qarun.

The increase in salt content of Lake Qarun with time

The effect of the fluctuation in the water level of the lake can be removed if we examine the salt content in the same period. Ball (1939) estimated the salt content of Lake Qarun in some years in the period from 1906 to 1932 and his values are reproduced in Table 2 together with the values calculated by the author for 1954 and 1970. It is clear from Table 2 and Figure 3 that the salt content was increasing with time and that the drop observed in some years is due to imperfect sampling and faulty calculations. The annual increase varied from year to year according to the variation of the volume of inflowing

Table 2. The salt content of Lake Qarun and its annual variation estimated in some years from 1906 to 1970

	Salt content × 10^{-9} kg			Salt content × 10^{-9} kg			Salt content × 10^{-9} kg	
Year	Value	Annual increase	Year	Value	Annual increase	Year	Value	Annual increase
1906	10·5		1923	16·8		1929	18·8	
		+0·3			−1·2			−0·2
1918	14·1		1924	15·6		1930	18·6	
		+1·3			+1·5			+1·2
1919	15·4		1925	17·1		1931	19·8	
		+0·3			+1·1			+0·6
1920	15·7		1926	18·2		1932	20·4	
		−0·1			+0·2			+0·2
1921	15·6		1927	18·4		1954	25·83	
		+0·6			+0·5			+0·5
1922	16·2		1928	18·9		1970	33·24	
		+0·6			−0·1			
1923	16·8		1929	18·8				

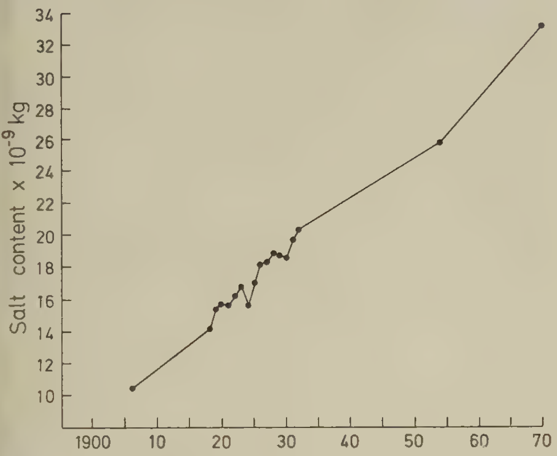

Figure 3. Variation of the salt content of Lake Qarun from 1901 to 1970.

drainage water to the lake. However, for short term variations it may appear that the annual increase in some years (1918–19 and 1924–26) was very high and seems to be exaggerated. This can be demonstrated by taking, as an example, the increase in one of these years (1918–19) which was $1{\cdot}3 \times 10^9$ kg. This amount is supposed to be conveyed to the lake by 1300×10^6 m^3 of drainage water taking its average salinity as 1 ‰. In the same time the lake is supposed to lose 420×10^6 m^3 of water through evaporation (Meshal, 1973). It follows that the lake had a net water gain of 880×10^6 m^3 which is larger than the whole volume of lake water in that year. On the other hand, there was a drop in the estimated salt content in other years (1921, 1924, 1929 and 1930, Fig. 3). This can be ascribed to the overestimation of the salt content in the preceeding periods as well as to the imperfection of sampling. Nevertheless, when the variation of salt content is averaged over a relatively longer period, it becomes more consistent and shows a persistent increase with time. The average annual increase was 370×10^6 kg during the period from 1906 to 1920; 290×10^6 kg from 1920 to 1930; 300×10^6 kg during 1930–1954 and and 460×10^6 kg in 1954–1970.

The control of the water level of Lake Qarun

The proper use of Lake Qarun as a receiver of drainage water and as a productive fishing area requires the control of its water level and the prevention of the increase of salinity. The control of the water level is essential for improving the irrigation and drainage systems in the province as well as securing the surrounding regions against the lake flood. Since these are the urgent needs, a plan was made to lower the lake level and control it at a constant value of −44·30 m. The excess of drainage water was conveyed to another basin called Wadi El-Riyan. El-Riyan (Fig. 1) is a depression of roughly the same area as Lake Qarun and its level varies from 0 to 50 m below sea level. The plan was in effect since December 1973 and the water level of Lake Qarun started to decrease gradually and was controlled at −44·30 m by the end of 1974.

The water level of Lake Qarun can be maintained constant as long as there is no net water gain or loss to or from the lake, i.e. $E = I + G + P$ where I is the inflow of drainage water, G the seepage to the lake, E the evaporation and P the precipitation. Of these, the only term which can be controlled is the influx of drainage water. The author studied the water balance of Lake Qarun corresponding to a water level of −44·30. It was found that the lake gains annually $67{\cdot}8 \times 10^6$ m^3 of water from seepage and $1{\cdot}8 \times 10^6$ m^3 from precipitation while it loses $437{\cdot}6 \times 10^6$ m^3 by evaporation. It follows that the water level can be kept constant if the lake receives 368×10^6 m^3 of drainage water per year.

Forecasting the salinity of Lake Qarun

The control of the water level of Lake Qarun at a constant value of −44·30 m will lead to a definite increase of salinity with time. The salt content and the average salinity which are expected in future may be calculated on the assumptions that:

1. The salinity of drainage water is taken as 0·96 ‰.
2. Drainage water contributed to the lake a total of $1{\cdot}155 \times 10^9$ kg of salts during the period from 1971 through 1973 and the water level of the lake was fluctuating around −43·89 m.
3. During 1974, which can be regarded as a transition period, the flow of drainage water to the lake started to be controlled. The mean water level was −44·10 m corresponding to a volume of 1004×10^6 m^3.
4. Starting from 1975 the water level is kept constant at −44·30 m at which level the lake has a volume of 958×10^6 m^3. The lake will receive an annual amount of drainage water of 368×10^6 m^3 which contains 353×10^6 kg of salts.

Table 3 shows the calculated salt content and the average salinity which are forecasted in the next 75 years (1975–2050). The increase of salinity is about

Table 3. The forecasted salt content and average salinity of Lake Qarun at the end of the indicated years 1975–2050.

Year	Salt content $\times 10^{-9}$ kg	Salinity ‰	Year	Salt content $\times 10^{-9}$ kg	Salinity ‰
1975....	35·1	35·7	2020	51·0	51·3
1980....	36·9	37·5	2030	54·5	54·7
1990....	40·4	41·0	2040	58·1	58·2
2000....	43·9	44·5	2050	61·6	61·6
2010....	47·5	48·0			

0·35‰ per year except in the transition period of 1974/1975 when the increase is much higher due to the appreciable decrease in volume. It can be concluded from Table 3 that fish which cannot tolerate a salinity more than 40‰ will be seriously threatened and may disappear from the lake within 15 years. If the salinity continues to increase at its present rate, the fisheries of the lake will steadily decline. Only fauna and flora which can tolerate salinity more than 60‰ will survive in Lake Qarun by the year 2050. It is expected that the lake would become a "dead" water body if the problem of the salinity increase remains unsolved.

Proposed solutions for the problem of salinity increase in Lake Qarun

At constant water level, the salinity of Lake Qarun remains constant as long as there is no change in its salt content. Hence, in order to stop the salinity increase the total amount of salts conveyed to the lake through drainage water should be removed from the lake water every year. As a proposal, this can be achieved by removing a certain volume of lake water that contains the same amount of salts. This volume, V_L, can be calculated as:

$$V_L = V \cdot S/S_L$$

where V, S are the volume and salinity of drainage water and S_L is the salinity of lake water. If we take the 1975 numerical values of the terms in the above equation ($V = 368 \times 10^6$ m^3, $S = 0{\cdot}96$‰ and $S_L = 35{\cdot}7$‰) then the volume of lake water which should be removed is $9{\cdot}9 \times 10^6$ m^3 per year. When this volume is removed from the lake, its salt content and consequently the salinity would remain constant. A convenient method of doing that is to isolate suitable regions of the lake from its main water body. The isolated regions are then left to evaporate for a certain period after which the water level will fall below that of the lake itself. A volume of lake water equal to that lost by evaporation is then allowed to flow to these regions.

The most suitable regions which can be easily isolated from the lake are the region A in the extreme western of end of the lake and the water pockets C, D, E and F located along its northern side (Fig. 4). This is because the area A is partly isolated from the lake by a natural land intrusion where the lake is only 500 m wide and 2 m deep. Similarly, the northern water pockets are connected to the lake by narrow and shallow openings of about 100 m width and 0·2 m depth. These openings are usually silted by sand and need frequent dredging and hence can be easily closed without appreciable costs. The isolation of each region can be made by constructing a dam across its connection with the lake. The proposed dam would be provided by a sluice-gate through which lake water flows to the isolated area. Assuming the rate of evaporation as 1·9 m/year (Meshal, 1973), the water level in the isolated parts would drop by this value below that of the lake proper. It should be taken in consideration that the lake receives continuous inflow of drainage water to compensate for its loss by evaporation. Table 4 shows the areas of the regions to be isolated, their annual capacity for receiving lake water and the total amount of dissolved salts which can be removed from the lake to each region. If the gates are closed for a one-year period the isolated parts are supposed to lose $8{\cdot}6 \times 10^6$ m^3 of water through evaporation corresponding to a drop in water level of 1·9 m. Consequently, an equivalent volume of lake water can be allowed to flow from the lake carrying 309×10^6 kg of salts to the isolated regions. This means that the salinity of the lake would increase but with a rather slow rate less than 0·05‰ per year until it reaches equilibrium value of about 41‰.

Table 4. Areas of the regions to be isolated from Lake Qarun and the volume of lake water and the quantity of salts to be removed from the lake to each region per year.

Region	Area km^2	Amount of lake water to be conveyed to each region per year: Volume $\times 10^{-6}$ m^3	Salt content $\times 10^{-6}$ kg
A..........	2·50	4·75	170
C..........	0·30	0·57	20
D..........	0·60	1·14	41
E..........	0·90	1·71	61
F..........	0·25	0·48	17
Total.......	4·55	8·65	309

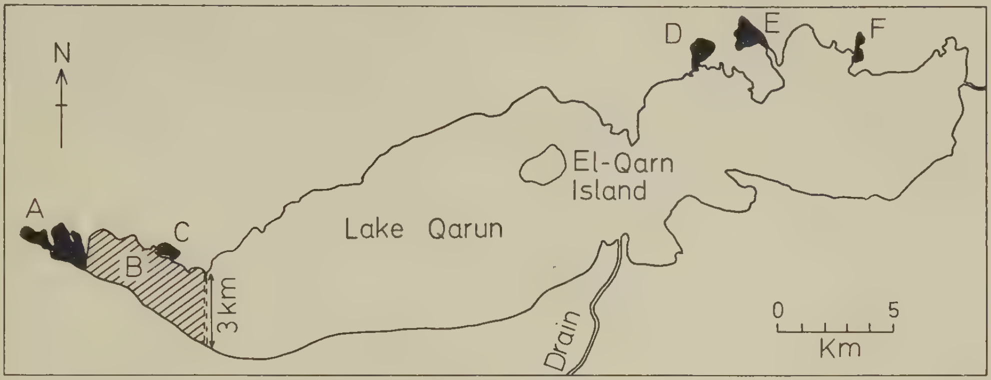

Figure 4. Proposed regions to be dammed and isolated from the main water body of Lake Qarun.

A complete control of the salinity of Lake Qarun can be obtained by an alternative project although it may cost more than the proposal discussed above. The idea of this project is to dam over a relatively larger portion of the western part of the lake (area A + B in Fig. 4). The dam would have a sluice-gate and to be constructed in a site where the lake is about 3 km wide and 3 m deep. The portion to be isolated has a surface area of about 15 km^2 and is estimated to lose $28 \cdot 5 \times 10^6$ m^3 of water per year by evaporation. This would cause its water level to fall by 1·9 m below that of the main lake. The required volume of lake water can then be allowed to flow from the lake to the dammed region. This provide means for complete control of the salinity of the lake proper. Thus, removing a volume of $28 \cdot 5 \times 10^6$ m^3 of lake water would reduce its salt content by 1017×10^6 kg of salt and decrease the salinity by 1‰ in the first year. The salinity of the lake proper would then assymptotically approach the equilibrium value of 12·4‰.

The isolated regions can be used as a reservoir for high salty water from which salts can be extracted.

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The growth at moulting of crawfish *Jasus tristani* at Tristan da Cunha, South Atlantic

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Growth increments of moulted crawfish *Jasus tristani* were recorded from animals tagged during 1971–73 at Tristan da Cunha, Nightingale and Inaccessible Islands in the South Atlantic Ocean. A decline in growth increment with size was observed for once-moulted animals of both sexes at Tristan da Cunha, with mean carapace length increments for males and females of 5 and 1 mm respectively. Growth increments of this magnitude were similar to those recorded for the South African species *Jasus lalandii*, over a similar size range.

Introduction

Exploitation of the palinurid *Jasus tristani* Holthuis is the principal source of revenue of the remote Dependency of Tristan da Cunha (37°13′S 12°27′W) in the southeast Atlantic Ocean, and a knowledge of growth is essential for determining sustainable yields. The growth rates of *J. tristani* are unknown. The construction of decapod growth curves is difficult for it is not possible to age the animals, and the growth rate has two components, frequency of moulting, and increase in size at moulting. The unimodal length frequency distributions of *J. tristani* (Roscoe, unpublished) indicate considerable overlapping of age groups, and year classes cannot be identified. This paper presents data on growth of adult Tristan crawfish at moulting, obtained by tagging the commercially fished stocks at the three northern islands and associated islets of Tristan da Cunha, namely Tristan da Cunha (Tristan), Inaccessible and Nightingale Islands and at Gough Island (40°19′ S 9°56′W) during a survey of the Dependency's crawfish stocks.

Material and methods

Adult crawfish were selected at sea from commercial catches during 1971–1973. They were marked with a numbered flexible dart tag inserted between the second and third abdominal terga, and returned to the sea. Fishermen were rewarded for returning marked crawfish. Moulted crawfish were detected by the deformation of the exoskeleton at the point of insertion of the tag, and the increase in carapace length after moulting was used as the measure of growth. Carapace length was measured from the rostrum tip to the posterior edge of the carapace. All the crawfish were recovered within a few kilometres of their release points. The numbers of tagged crawfish released and recovered up to mid 1975 at the four islands are presented in Table 1. The proportion of marked crawfish returned after moulting was small, ranging from about 0·2% of those released

Table 1. Summary of tagged crawfish released in 1971–73 and recovered up to mid 1975.

Location	Numbers released	Total number returned	Numbers of once moulted crawfish recovered males	females
Tristan……	2387	320	74*	34*
Inaccessible..	966	22	6	1
Nightingale..	1035	50	13*	4
Gough……	1860	22	3	0
Totals…….	6248	414	86	39

* Signifies that a regression analysis for moult increment was undertaken.

at Gough Island to 5% at Tristan. Some few crawfish were considered to have moulted twice, and in other cases only the tagged abdomen was returned and no information on growth was available.

Results

The relationships between original carapace length and increment for male crawfish from Tristan and Nightingale are plotted in Figure 1(a), (b). The regression equations of increment on original carapace length for each sex are listed in Table 2. The significant ($P < 0{\cdot}001$) negative slope of increment on length of once-moulted Tristan males indicates that the growth increment decreases with carapace length. For Nightingale males, the lack of a significant relationship between increment and length in this small sample suggests that the increment is independent of length at tagging, and that on moulting there is a mean increment of 5 ± 2 mm.

Six males from Inaccessible, original length 79–103 mm, had a mean increment of 4 ± 1 mm.

For females from Tristan, growth increments were also significantly negatively correlated with length (Table 2). The mean increment (1 mm) was very much smaller than for males of the same size range (Fig. 1c). Only four once-moulted females were returned from Nightingale, and these increments were also low, that is, between 0 and 2 mm.

Discussion

The growth increments for male *J. tristani*, of original carapace length 73–109 mm from Tristan and Nightingale Islands, are similar to those observed for male *Jasus lalandii* (M. Edw.) of similar size at Dassen Island, off the South African West coast, by Newman and Pollock (1974a). They recorded mean increments, independent of length, ranging from 2·8 mm, in deeper water devoid of kelp, to 5·5 mm in an area adjoining shallow inshore waters where kelps were abundant. Newman (1972) reported mean increments ranging from 4·5 mm for the 70–79 mm length class down to 2·1 mm for the 100–109 mm class for *J. lalandii* at the Cape Peninsula. Street (1969) reported mean annual increments of 5 mm, independent of original length, in similarly sized male *Jasus edwardsii* (Hutton) from southern New Zealand.

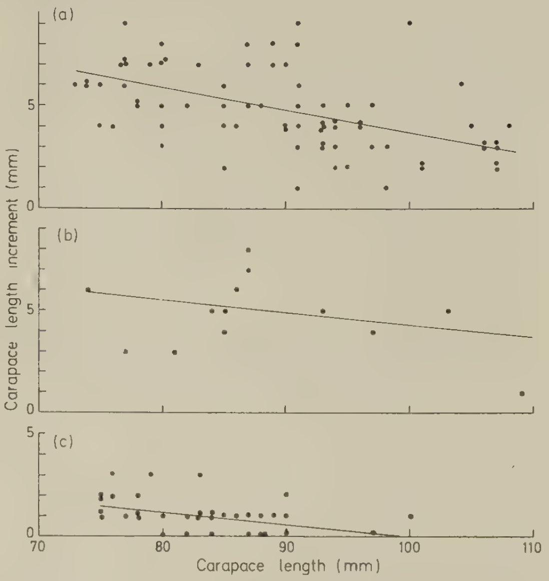

Figure 1. The relationship between original carapace length and moult increment for (a) Male crawfish at Tristan da Cunha. (b) Male crawfish at Nightingale Island. (c) Female crawfish at Tristan da Cunha. Lines fitted by regression analysis.

The limited data for male *J. tristani* from Inaccessible Island suggest that the mean increment may be less than that for Tristan or Nightingale crawfish. Roscoe found in 1971–73 that the mode of the size frequency distribution for Inacessible males was markedly lower than for Tristan or Nightingale males, and Rowan (unpublished) noted that Inaccessible crawfish were smaller when exploitation commenced in 1949.

In South African waters, growth rates of *J. lalandii* were found to vary substantially, and these were linked with environmental factors, such as the amount of benthic fauna available as food. Although some populations of *J. tristani* and *J. lalandii* have similar growth patterns, there is a marked difference between the environments of the coastal *J. lalandii*

Table 2. Regression equations of increment on original carapace length for crawfish

Location	Sex	Number	Regression equation	Correlation coefficient r	P
Tristan.................	males	74	$y = 14{\cdot}56 - 0{\cdot}11x$	−0·52	<0·001
Nightingale............	males	13	$y = 10{\cdot}33 - 0{\cdot}66x$	−0·34	< 0·1
Tristan.................	females	34	$y = 5{\cdot}99 - 0{\cdot}06x$	−0·43	<0·01

and the oceanic *J. tristani*, which has a greater vertical range. Whereas *J. lalandii* are found in depths of up to 60–70 m, *J. tristani* have been caught in depths of well over 360 m. The rate of growth of *J. lalandii* is related to the abundance of mytilids, which are a major component of the crawfish's diet (Newman and Pollock, 1974a). In contrast to *J. lalandii*, Heydorn (1969) and Rowan found that the diet of *J. tristani* appeared to be vegetarian, and that the benthic fauna was sparse; with mytilids being absent (Soot-Ryen, 1960).

The growth of moulting of mature female *J. tristani* apparently declines with size over the size range 75–100 mm, and is considerably less than that of adult males at the three islands. Similar results were obtained for *J. lalandii* at the Cape by Newman (1972), and Street (1969) reported that mature female *J. edwardsii* grew much slower than males. This slow rate of growth in mature females, widely observed in palinurids, is attributed to the diversion of production to oogenesis rather than increase in biomass.

There is not yet sufficient information to construct growth curves, but preliminary analysis of our data and that of Heydorn (1969) strongly suggests that growth by moulting occurs annually in adult *J. tristani*, as is the case for *J. lalandii* (Newman and Pollock, 1974b).

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On the shoaling behaviour of sardines *(Sardina pilchardus)* in aquaria

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Sardines of a similar size formed one shoal when kept under suitable conditions and grew well. Sardines with a wide size range formed two shoals or one shoal partly segregated by size; one dense shoal was formed only when the fish were disturbed. When the size range was large, only the larger fish grew well; the smaller fish died. Shoaling between sardines (or between sardines and sprats or anchovies) of markedly different size appears to be exceptional under natural conditions.

Introduction

A comparison was made between the shoaling behaviour of sardines (*Sardina pilchardus*) of similar and markedly different lengths when kept in aquaria. It was hoped that these studies might contribute to a better understanding of the shoaling behaviour of sardines in the sea.

Material and methods

Six experiments were carried out using sardines taken from commercial purse seine catches on grounds close to the Institute at Split. The details are summarized in Tables 1 and 2. Usually two samples were taken from each haul, the first for aquarium observations and the second for length measurements. In one sample (No. 5) the fish were used for both purposes. In experiments 1–5 the fish were taken from single catches but in experiment 6 the fish came from two catches.

A grand total of 988 sardines were used in the experiments (Table 2) and 977 sardines were measured (Table 1). The mean total lengths ranged from 10·2 to 16·3 cm. As shown in Figure 1 the fish used in experiments 1–5 had a homogeneous and almost symmetrical length distribution, although samples 2 and 3 had a wider length range and a higher coefficient of variation. In experiment 6 the length distribution was heterogeneous.

The sardines were kept in large rectangular tanks (295 × 119 × 120 cm deep). In experiments 4, 5 and 6 (in part) the fish were previously kept in much smaller rectangular tanks. All the tanks were provided with running unfiltered sea water.

The fish were fed at least four times a day with moistened fish meal to which vitamins (vitamin A, thiamine, riboflavin, pyridoxine, nicotinamide, d-calcium pantothenate, ascorbic acid and vitamin D) were added. Uneaten food was removed when cleaning the tank. The smallest particles floated at the surface and were carried away in the outflow; these particles were sometimes eaten by fish in bad condition.

As shown in Table 2 the initial water temperatures

Table 1. Data on sardine samples used for aquarium observations.

Sample No.	Date	Number of fish	Length data Range cm	Mean cm	Standard deviation cm	Coefficient of variation %
1.............	27 May 1962	58	13·1–16·9	15·6	0·80	5·1
2.............	17 Jul 1963	237	6·6–12·6	10·2	0·98	9·6
3.............	10 May 1964	80	9·9–15·3	13·3	1·08	8·1
4.............	23 Oct 1966	159	10·0–13·4	12·1	0·68	5·6
5.............	22 Jun 1967	58	13·7–16·1	14·9	0·65	5·1
6a...........	16 Jul 1969	105	14·2–17·7	16·3	0·59	3·6
6b...........	26 Jul 1969	280	8·3–13·0	11·0	1·03	9·4
6a & 6b pooled..		385	8·3–17·7	12·4	2·57	20·6

Table 2. Number of fish and initial temperature conditions for the aquarium experiments.

Experiment No.	Date	Initial temperature °C	Initial number of fish
1.	27 May 1962	19·0	88
2.	17 Jul 1963	25·0	245
3.	10 May 1964	18·0	239
4′	26 Nov 1966	17·0	248
5′	22 Jun 1967	20·3	58
6a.	17 Jul 1969	20·8	35
6b.	26 Jul 1969	22·0	75

′ The fish were kept for some time in small tanks.

ranged from 17° to 25°C. In experiment 4 the temperature was always maintained above 14·5°C and in experiments 5 and 6 the temperature was always above 13·5°C.

Some fish were removed from the tanks during the experiments and the dates are indicated in Figures 2 and 5. The fish removed were not included when estimating percentage mortalities.

Other samples from commercial purse seines or shore seines catches taken from the central part of the eastern Adriatic are referred to in the Discussion. Details of these samples are given in Tables 3 and 4, and Figures 6, 7 and 8.

Results

Behaviour and mortality of sardines of similar lengths

Observations were made only on the fish kept in a large tank; in small tanks, only small fish shoaled (Mužinić, 1966). At first the fish only shoaled when frightened, but later they shoaled whenever conditions were suitable for polarization (Mužinić, 1966). The sardines formed one shoal and swam round the tank in one direction. Rarely, the shoal split up and when this did happen the two shoals joined up again quickly. After an initial highly variable mortality (Fig. 2a–e) there were many weeks with few or no deaths: deaths in September in experiment 5 were probably related to maintenance work in the tank room.

In those experiments begun earlier in the fishing season (1, 2, 3 and 5), sardines were kept successfully for many months (Fig. 2a–c, and e). They took food voraciously, although not in the initial phase of captivity, and after an initial weight loss grew in length and gained in weight. In the small fish in experiment 2 growth was intensive and the scales developed a large marginal growth zone (Mužinić, 1966).

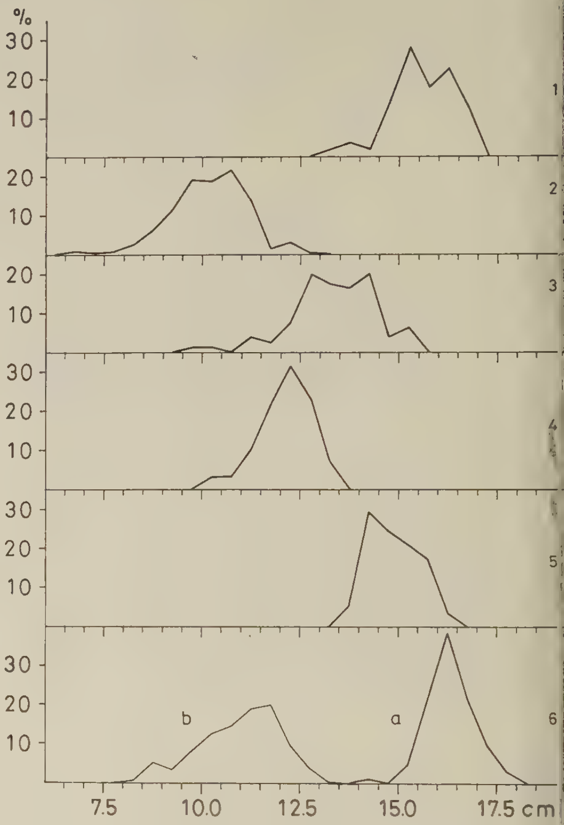

Figure 1. Length distributions of sardines in the samples used for aquarium observations.

It was shown earlier (Mužinić, 1964) that the later mortality followed a winter fall in temperature and coincided with the onset of sexual maturity, but mortality persisted during the subsequent rise in temperature.[1] The winter mortality also occurred in experiments 4 and 5, although the temperature was kept above 14·5° and 13·5° respectively (Fig. 2d and e).

Behaviour and mortality of sardines of different lengths

The two samples used in experiment 6 had very different means and the length distributions did not overlap (Table 1 and Fig. 1). The length distribution of the large sardines was symmetrical but that of the small sardines was skewed.

After being kept for one day in small tanks, the 35 large sardines that survived were transferred to the big tank. At first they only shoaled when

[1] An increase in mortality occurred earlier in experiment 3 and was probably due to work in connection with the FAO/GFCM seminar on sardine tagging. A more rapid increase in mortality is evident later.

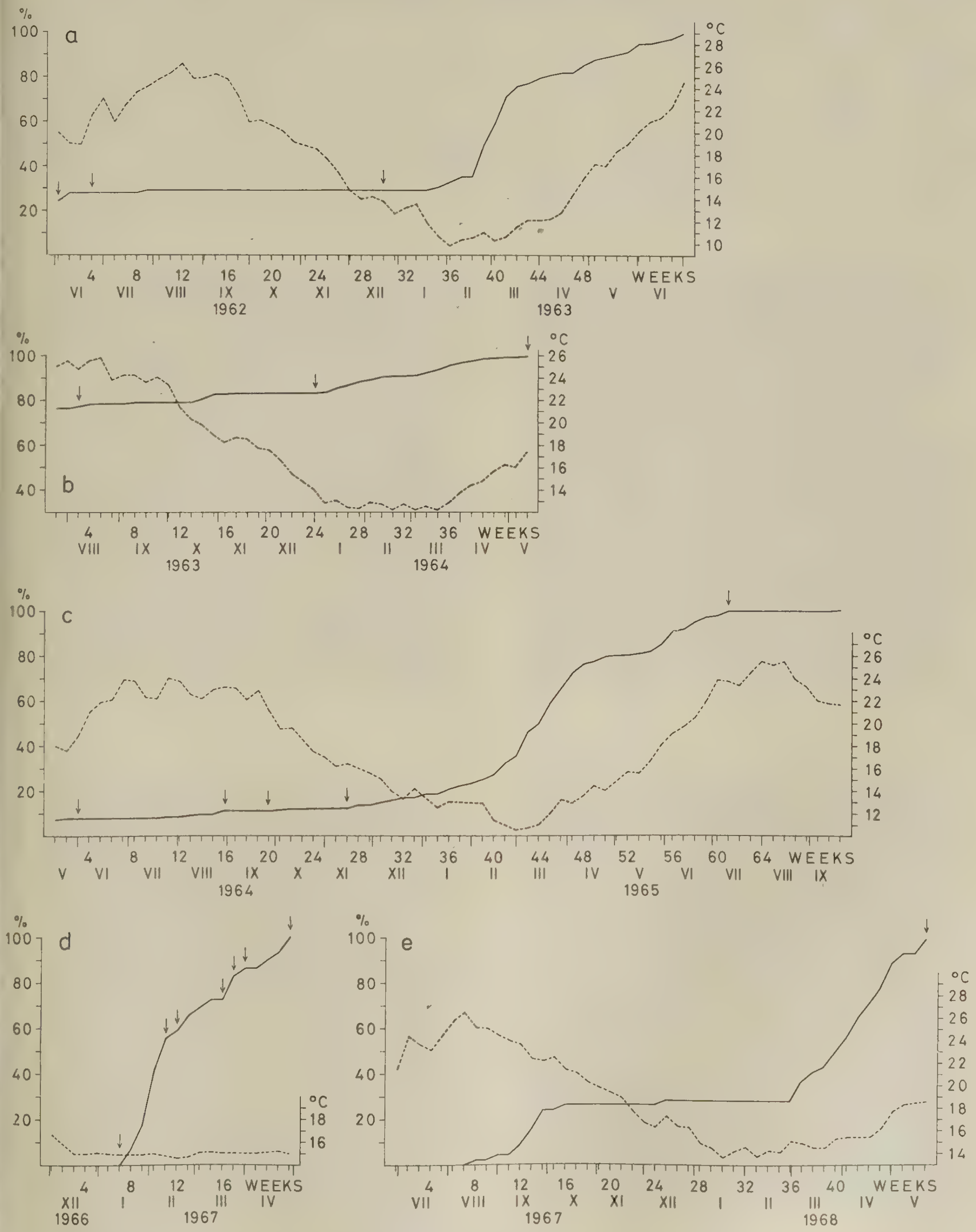

Figure 2a–e. Cumulative mortality of sardines and temperature (broken line) in experiments 1–5. Interventions and accidents are marked by arrows.

frightened but after a few days the fish formed a shoal. The fish swam round the tank in a clockwise direction, and the shoal sometimes broke up along the shorter sides of the tank.

Nine days later 75 small sardines were put directly into the tank. Shortly afterwards both large and small fish milled in a clockwise direction, but separately, the small fish being more loosely packed and closer to the surface. On the following day the fish formed one or two shoals and continued to swim round the tank in a clockwise direction; there were then 34 large and 70 small sardines alive. This be-haviour pattern was repeated on subsequent days. Even when shoaling separately, the small and large sardines swam in the same direction. However, in another experiment small sardines changed their swimming direction when shoaling with large sardines (Mužinić, unpublished).

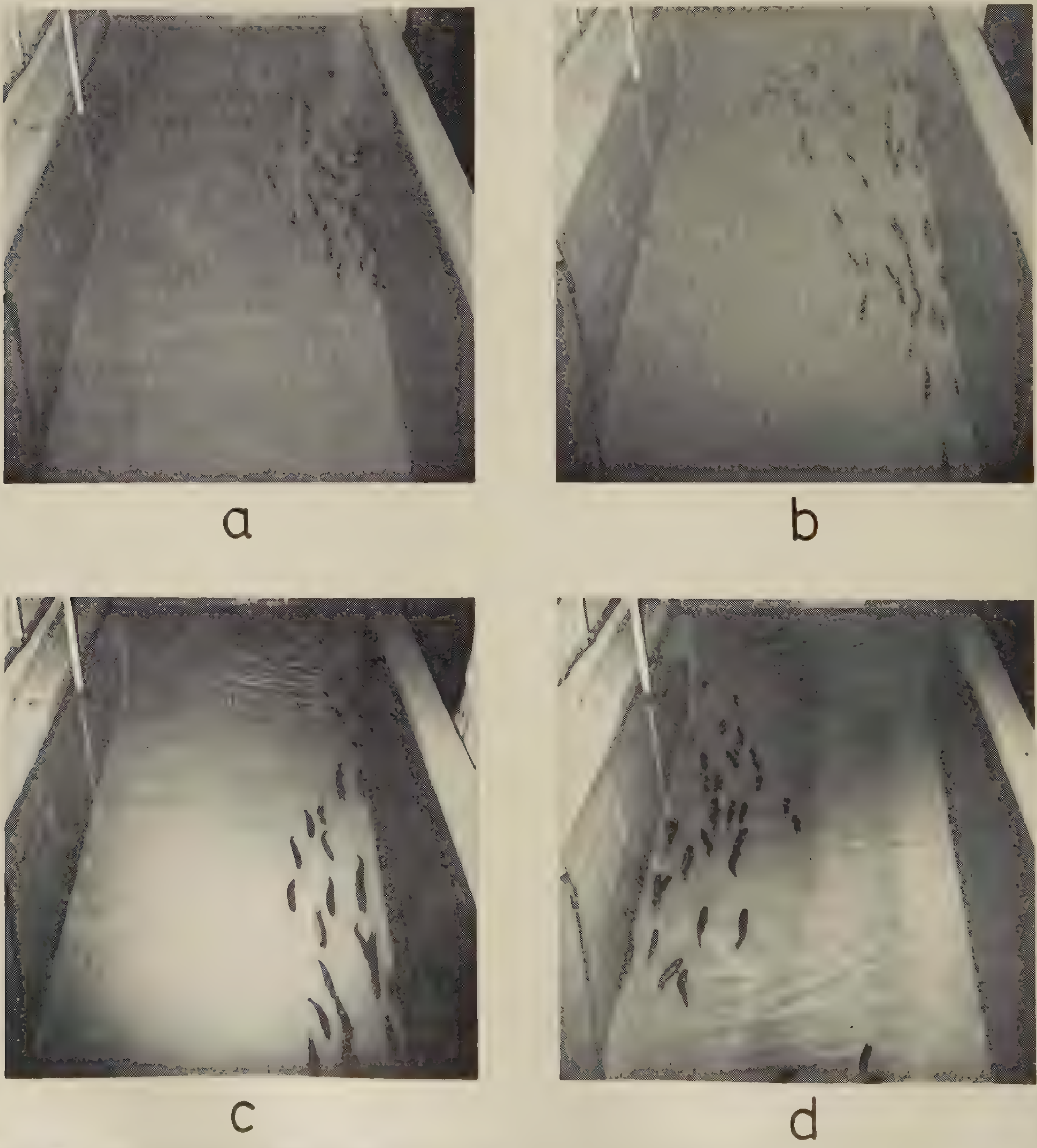

Figure 3a–d. Photographs of a group of small and large sardines to show stages leading to the formation of tw separate shoals of small and large fish. a, b and c, smaller fish tending to be left behind; d, two shoals, the smalle fish swimming at the far end of the tank, and near the surface.

When large and small sardines shoaled together the small fish kept closer to the surface and were often left behind. This represented a transitional stage towards complete segregation into two shoals with the smaller fish up near the surface (Fig. 3a–d). Sometimes a few small fish joined the shoal of large fish and vice-versa. At times the two shoaling groups circled side by side, the big fish near the walls of the tank, the smaller fish being looser and closer to the surface. When a shoal of small and large fish was disturbed it became more closely packed (Fig. 4).

The large sardines suffered a 67% mortality during their first day when held in small tanks. But after being transferred to the big tank there were only 6 further deaths (17%) until the onset of the late mortality phase in the 28 week (second half of January) in relatively warm water as shown in Figure 5. The same figure shows that the small sardines were dying throughout the first 15 weeks, when the cumulative total mortality reached 92%. Their pattern of mortality was therefore very different from that of the large sardines in the same tank and from that of the sardines in experiments 1–5 (Fig. 2a–e).

A few small sardines started feeding after one week but they never fed well. Some of the large fish started to feed at the same time (after more than two weeks in the tank) and a week later they were feeding vigorously. The small fish did not concentrate at the spot where the food was thrown. Their feeding might have been handicapped, at least to some extent, by the intensive feeding of the big sardines. Small sardines from experiment 2 started to take food early, and later fed very intensively and grew excellently in the same tank.

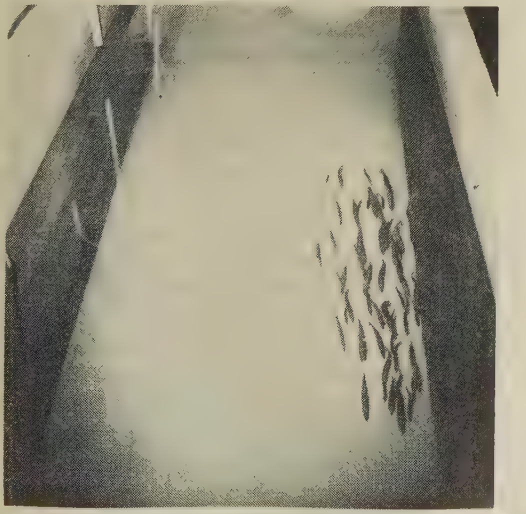

Figure 4. Small and large sardines forming an integrated shoal after being disturbed.

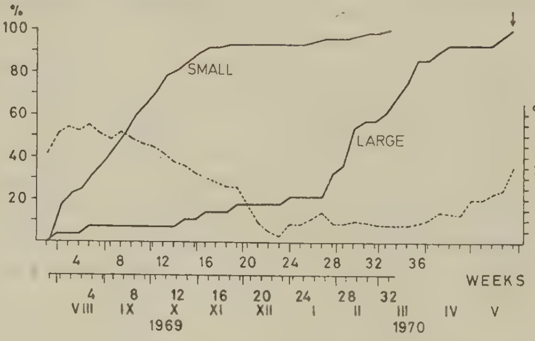

Figure 5. Cumulative mortality of large and small sardines and the temperature (broken line) in experiment 6. Interventions and accidents are marked by arrows.

Discussion

The shoaling behaviour of sardines of a similar length differed from that of fish with a wide range of size. The former made one shoal, but the latter rarely formed a dense integrated shoal and then only when disturbed. To shoal with the large fish the small sardines had to change their swimming direction when it was different from that of large sardines, which points to some flexibility in the behaviour of this species. The modifying effect on behaviour patterns by the presence of other individuals of the same or other species has been called "social interference" by Miyadi (1960).

When forced to live with the large fish in a rather limited space the small sardines did not feed well and eventually died.

The fact that small and large sardines often formed separate shoals in the large tank, in spite of the limited space, and that the small fish took little food and suffered high mortality suggests that a shoal of markedly different sizes of fish is not usual in the sea. The small fish would have to use more energy to keep up with the large fish, both in the tanks and in the sea.

Fish often shoal by size. Examples are: *Jenkinsia lamprotaenia* (Breder, 1951); *Sardinella aurita* (Ben-Tuvia, 1960a); sardines (Tardent, 1962); *Scomber scombrus* (Sette, 1950); *Thunnus albacares* and *Katsuwonus pelamis* (Broadhead and Orange, 1960); *Thunnus thynnus* (Mather, 1963); *Sarda sarda* (Demir, 1963); *Euthynnus alleteratus* (Marchal, 1963). Uniformity of size is not unexpected, because coherent orientated shoals can only be formed by individuals which swim at about the same speed.

However, there are some records of shoals with a varied size composition; examples are *Sardinella maderensis* (Ben-Tuvia, 1960b) and *Thunnus thynnus*

(Mather, 1963). Underwater observations (MacKay, 1967) have shown that mackerel (*Scomber scombrus*) of different sizes formed one shoal within a purse seine.

Shoals with a varied size composition often show vertical or horizontal segregation. This has been shown for *Engraulis japonicus* (Kimura, 1934); *Jenkinsia lamprotaenia* (Breder, 1951); *Clupea harengus* (Schäfer, 1955); sardines (experiment 6 in the present investigations); *S. scombrus* (Sette, 1950); *Neothunnus macropterus* (Schaefer, 1948) and *T. thynnus* (Mather, 1963). When vertically segregated the small fish kept closer to the surface. Furnestin (1953) recorded a vertical segregation in Moroccan sardines, and Johnson (1970) in the sprat *Clupea sprattus:* here again the fish in the upper layer were smaller. Tester (1952) found that large and small tunny (*Euthynnus yaito*) formed one shoal in a live well, although there was no overlap in the size distributions of the two groups. When circling the large fish kept to the outside, as was sometimes observed with sardines (experiment 6).

Breder (1959) thought that vertical segregation might be the first stage in the separation of a shoal into two groups of more uniform size. Pelagic shoals of a varied size composition found under certain conditions may not represent stable groups, and such shoals may have only transitory advantages for the smaller fish.

The more uniform size composition often observed in pelagic fish shoals may arise because they break and form up fairly readily. Shoals have been recorded as splitting up; examples are young Californian sardines (*Sardinops caerulea*) and other pelagic species (Phillips, 1952). In the presence of a predator a shoal of anchovies (*Engraulis mordax*) broke up and reformed again immediately (Phillips, 1952). From the dispersion of tagged fish throughout the stock, Brock & Riffenburgh (1960) supposed that there was a substantial interchange of individuals among shoals, and Cushing and Harden Jones (1968) also concluded that shoals were not permanent.

In such a vulnerable fish as the sardine there are probably frequent accelerations in swimming speed which will result in a shoal of varied size composition becoming broken down into smaller, more uniform, and thus more coherent shoals. A markedly heterogenous size composition is relatively rare in the commercial sardine catches in the central part of the eastern Adriatic (Mužinić, 1954, unpublished). The size distributions of some of these samples are shown in Figure 6, and the data are summarized in Table 3. The lower of the standard deviations (samples 6–8) are similar to some of the samples used in the aquarium observations (samples 3 and 6b, Table 1). In one sample taken in coastal waters (sample 5, Table 3) the standard deviation approaches that obtained when mixing two of the samples used in the aquarium observations (samples 6a and 6b, Table 1). The aquarium observations led to the hypothesis that sardine shoals of such a varied length composition would not persist for any length of time under natural conditions. If the hypothesis is correct, those samples in Table 3 with the higher standard deviations (samples 2, 3, 4 and 5) might not be expected to form permanent coherent groups. These samples may have been taken from aggregations formed under the influence of artificial lights.

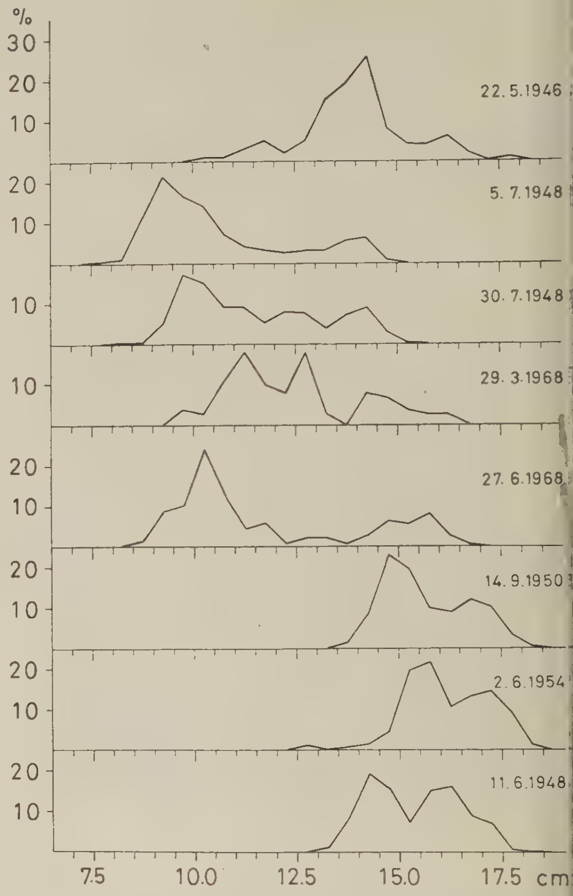

Figure 6. Heterogeneous length distributions of sardines in samples from the central Adriatic.

There are some records of mixed species shoaling by size. Examples are: *Sardinops caerulea* with *Engraulis mordax* or other fishes (Phillips, 1952); *Katsuwonus pelamis* with *Neothunnus macropterus* (Schaefer, 1948), or *Thunnus thynnus* or *T. atlanticus* (Mather, 1963); *Euthynnus alleteratus* with *Auxis thazard* or *Sarda sarda* (Marchal, 1963).

Table 3. Data on heterogeneous sardine samples taken in the central part of the eastern Adriatic.

Sample No.	Locality	Date	Number of fish	Length data Range cm	Mean cm	Standard deviation cm	Coefficient of variation %
1...........	Kaštela B.	22 May 1946	102	10·3–17·7	14·0	1·33	9·5
2...........	Kaštela B.	5 Jul 1948	514	7·8–14·7	10·6	1·73	16·3
3...........	Kaštela B.	30 Jul 1948	387	8·0–15·0[1]	11·5	1·67	14·5
4...........	Kaštela B.	29 Mar 1968	100	9·7–16·4	12·5	1·67	13·4
5...........	Kaštela B.	27 Jun 1968	137	8·8–16·7	11·8	2·33	19·7
6...........	SW Brač I.	14 Sep 1950	319	13·6–18·3	15·7	1·06	6·8
7...........	NW Hvar I.	2 Jun 1954	252	12·7–18·4	16·2	1·03	6·4
8...........	Vis I.	11 Jun 1948	299	13·3–18·0	15·4	1·10	7·1

[1] The lengths were read to 0·5 cm below.

Some cases of a vertical species segregation by size were also recorded. In the open central Adriatic, fishermen using lights found large mackerel below sardines, the two groups differing by size (small mackerel appear thoroughly mixed with sardines).

Traces of a horizontal species segregation were recorded in a mixed polarized ring-shaped group of large sardines and small anchovies (*Engraulis encrasicolus*), the length distributions showing little overlapping in the aquarium under conditions not favouring typical shoaling (the fish were rather crowded and tended to form a typical shoal only when disturbed) (Mužinić, unpublished observations).

There are some records of one species mixing with small numbers of other species. Examples are: *Sardinops caerulea* with *Engraulis mordax* (Phillips, 1952) and sardines with small *Trachurus sp.* (Tardent, 1962). In some cases a difference in the size or in the swimming speed of the species was recorded, as shown by examples of one yellowfin (*Neothunnus macropterus*) shoaling with five tunnies (*Euthynnus yaito*) which are better swimmers (Van Weel, 1952) and one sardine shoaling with large mackerel (*S. scombrus*) (Tardent, 1962).

Samples containing mixtures of species (sprat, anchovy, sardines) of markedly different length composition have been taken from catches in the coastal waters of the central eastern Adriatic (see Figs. 7 and 8 and Table 4). The anchovies were usually smaller than the sardines. If two species of similar size swim at approximately the same speed, the mixed groups from which samples 3–7 and 9 were taken would behave as single species groups: the shoals would be unstable and would not persist as shoals under natural conditions. A critical swimming speed would lead to segregation by size or by species, and the laboratory experiments which showed differential mortality in sardines suggest that there would be little or no advantage to the smaller fish in a common shoal.

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The author offers her warmest thanks to the Com-

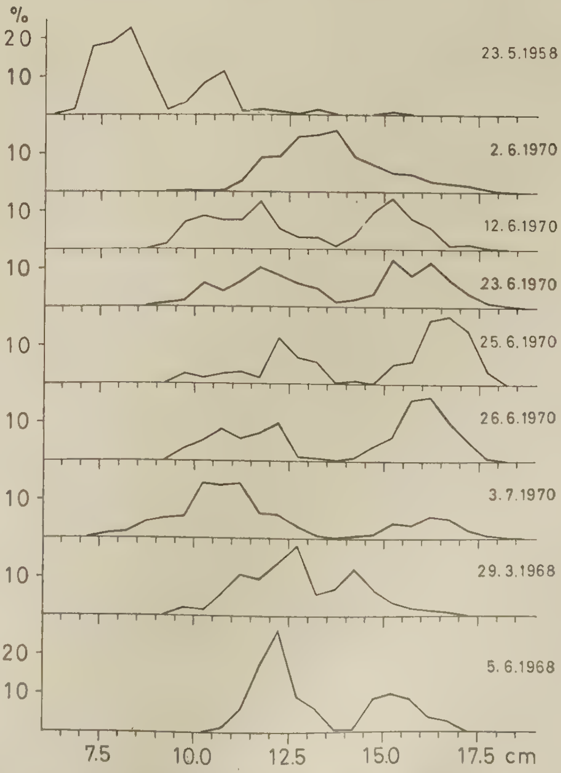

Figure 7. Heterogeneous length distributions of fish in mixed species samples from the central Adriatic.

Table 4. Data relating to mixed species samples taken in the central part of the eastern Adriatic.

Sample No.	Locality	Date	Number of fish sardine	Number of fish anchovy	Number of fish sprat	Length data Range cm	Length data Mean cm	Length data Standard deviation cm	Length data Coefficient of variation %
1	Novigrad B.	23 May 1958	63	0	106	6·7–15·3	8·7	1·44	16·5
2	Kaštela B.	2 Jun 1970	76	369	0	10·6–18·4	13·7	1·45	10·6
3	Kaštela B.	12 Jun 1970	95	131	0	9·0–17·7	13·0	2·27	17·4
4	Kaštela B.	23 Jun 1970	82	83	0	9·3–18·0	13·8	2·32	16·8
5	Kaštela B.	25 Jun 1970	74	45	0	9·6–17·8	14·9	2·32	15·6
6	Kaštela B.	26 Jun 1970	93	64	0	9·6–17·8	14·1	2·48	17·5
7	Kaštela B.	3 Jul 1970	146	202	0	7·6–18·1	12·0	2·56	21·3
8	Neretva Ch.	29 Mar 1968	100	100	0	9·7–16·8	12·9	1·49	11·6
9	Neretva Ch.	5 Jun 1968	53	100	0	10·8–16·9	13·3	1·67	12·5

mandant of the M/B "Predvodnik", A. Jončić; engineer, A. Dujmović; and members of the crew N. Mladinov, D. Prga and G. Cecić, as well as to the aquarist S. Vitaljić, for their untiring efforts in providing sardines.

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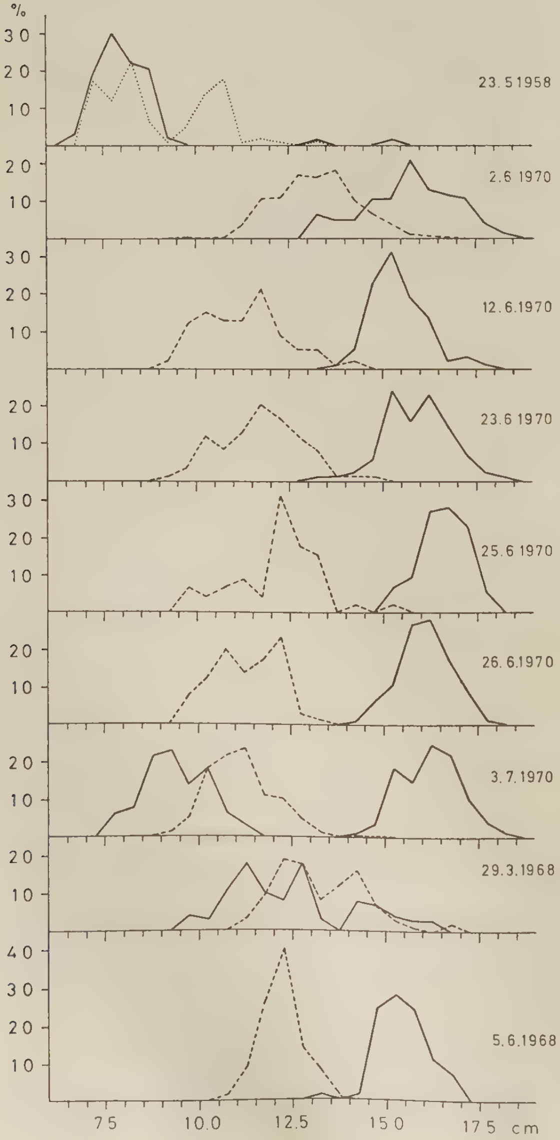

Figure 8. Length distributions of the species (solid line sardine, broken line anchovy, dots sprat) represented in the mixed species samples used in Figure 7.

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Does salinity influence the number of vertebrae developing in fishes?

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Using the cyprinodontid fish, *Fundulus majalis*, five lots of 44 embryos each were reared in jars from gastrulation to hatching in a controlled-temperature room at five different salinities (16, 21, 26, 31 and 36 ‰). Comparisons of mean vertebral counts show no statistically significant differences occurring between them and thus no salinity influence upon vertebral number is indicated. The literature from the field of salinity influence upon vertebral number in fishes is reviewed and it is concluded that there is little evidence, from the field or the laboratory, to support the generally expressed acceptance of salinity as an important environmental factor known to modify vertebral number in developing fishes.

Introduction

Whenever the environmental factors known to influence the number of meristic structures developing in marine fish embryos and larvae are listed, salinity is always included. When vertebrae alone are considered, observations of salinity influence are based primarily upon field studies showing a correlation between vertebral counts and salinities from different areas. Among authors who have reviewed the general field of meristic structure response to different environmental factors, conclusions about salinity influence on vertebral number vary from questionable (Tåning, 1952) to definite (Kinne, 1964; Fowler, 1970). Currently, there appears to be general acceptance of the idea that salinity is an important environmental factor in regard to influencing the number of vertebrae developing in fish.

This study is concerned with, 1) the response to different salinities by presumptive vertebral tissue in developing embryos of *Fundulus majalis* (Walbaum), and 2) a review of the literature concerned with the influence of salinity upon the number of vertebrae developing in fishes.

Materials and methods

Parent fish were collected by hand on the nights of 19 July 1971 (shore of Newport River, north side of Morehead City-Beaufort causeway) and 21 July (north side of Bogue Sound), placed in filtered sea water (Fahy, 1964) circulated through a 40 l aquarium (temp. = 22·0°–23·0°C; S = 31·0–33·0 ‰) and fed *Artemia* nauplii several times daily. To induce maturation of ova females were narcotized in tricaine methanesulphonate solution (0·055 g/l sea water) and daily intraperitoneal injections of chorionic gonadotropin hormone (one I.U./100 g body wt.) were administered (Joseph and Saksena, 1966). A scale was removed from the mid-ventral line immediately anterior to the vent and at each injection the syringe needle was inserted here. Fertilization of ova (Fahy, 1972) using two males and three females was accomplished during the night of 23 July after two to four hormone injections (temp. 22·5°C; S = 32·9 ‰). After 15 min eggs were removed to a temperature-controlled room (22·0°–23·0°C) with continuous indirect lighting. Parent fish were killed and preserved in ten percent non-acidic formalin.

The following morning 220 viable eggs were mixed thoroughly to provide homogeneous samples. Five lots of 44 embryos each were placed directly, without acclimatization, into separate, wide-mouth, glass jars containing 3·0 l filtered sea water, of differing salinities (16, 21, 26, 31 and 36‰). Salinities were obtained by diluting sea water of higher salinity with distilled water or by adding artificial sea salts in the case of the highest salinity. Salinities were checked daily by hydrometers. The embryos were reared at temperatures of 22·0°–23·0°C under continuous, indirect, cool-white, fluorescent lighting with 350 g of marble chips in an immersed, perforated, plastic container for stabilisation of pH. Temperature and salinity stratification of water were prevented by gentle mixing during routine observations (two to three times daily) of development, salinity and pH. Oxygen content of water was not regulated. In *Fundulus*, vertebrae are formed and are stainable before hatching. Several days after hatching began, the chorion was cut to release any unhatched embryos, thus permitting the vertebral column to straighten. Killing and subsequent preparation of specimens for staining have been described (Fahy, 1972). Complex vertebrae were counted as two. Vertebrae counts were statistically treated with an analysis of variance and *F*-test.

Results

During the experiment variations in the salinity readings of sea water in each of the five jars ranged from 0·7‰ (31·0‰) to 1·1‰ (26·0‰) and values for pH varied from 0·25 (21·0‰) to 0·50 (26·0‰) as derived from Table 1. In this table mortality rates are shown to have ranged from 2·3% (21·0‰) to 18·2% (26·0‰). Among the five lots there were differences in elapsed time between fertilization and appearance of certain structures (optic capsules, somites, pigment of eye, etc.). Embryos in 31·0‰ sea water usually showed a given structure first; those in 26·0‰ and 36·0‰ developed them next; embryos in 21·0‰ formed these still later and those in 16·0‰ showed them last. Hatching began 24 days after fertilization but it was sporadic and extended over several days; no pattern related to salinity was apparent. Most mortalities occurred three days after hatching began. Because of the limited time available to one of us (R.K.O.), the experiment was terminated as soon as practicable. An analysis of variance with the *F*-test (Table 2) indicated no statistically significant differences occurring among mean vertebral counts ($F = 0{\cdot}596$; $F_{0{\cdot}05} = 13{\cdot}52$).

Table 1. Mortality rates and ranges for salinity and pH readings in each of five jars of the experiment.

Experiment number	Percent mortality	Ranges salinity ‰	pH
1	4·5	15·7–16·7	7·49–7·79
2	2·3	20·9–21·8	7·54–7·79
3	18·2	25·8–26·9	7·55–8·05
4	4·5	31·1–31·8	7·62–8·09
5	13·6	36·2–37·0	7·62–8·05

Vertebral counts for the parent fish were: males, 34 vertebrae each; females, two with 34 vertebrae and one with 35.

Table 2. VS frequency distributions with percentage distributions in parentheses, number of individuals (n), mean, and variance (s^2) for embryos reared continuously in five different salinities with a table of analysis of variance and an *F*-test.

Salinity range ‰	VS distribution 33	34	35	36	n	Mean	s^2
15·7–16·7	7 (16·7)	21 (50·0)	14 (33·3)	0(0·0)	42	34·167	0·4837
20·9–21·8	4 (9·3)	20 (46·5)	19 (44·2)	0(0·0)	43	34·349	0·4231
25·8–26·9	3 (8·3)	23 (63·9)	9 (25·0)	1(2·8)	36	34·222	0·4063
31·1–31·8	5 (11·9)	20 (47·6)	16 (38·1)	1(2·4)	42	34·309	0·5117
36·2–37·0	3 (7·9)	26 (68·4)	8 (21·1)	1(2·6)	38	34·184	0·3705

Table of analysis of variance

Source of variation	d.f.	sum of squares	variance estimates
Between salinities	4	1·05	0·263
Within salinities	196	86·51	0·441
Total	200	87·56	

$$F = \frac{0{\cdot}263}{0{\cdot}441} = 0{\cdot}596 \qquad (F_{0{\cdot}05} = 13{\cdot}52)$$

Discussion

In the literature salinity is frequently considered to be equal in importance to temperature as an environmental factor influencing the number of vertebrae developing in fishes (Lindsey, 1962; Kinne, 1964; Fowler, 1970; Ali and Lindsey, 1974). The correlation usually noted is that increased salinity induces an increased mean vertebral number; it is stated, or implied, that the metabolic rate is reduced by increased salinity thus causing the increase in vertebral number. There are discrepancies between the actual findings of earlier investigators and their reported findings in later papers so that the foundation upon which claims for salinity influence on developing vertebral number are based is not sound. We present below the results and conclusions from cited field studies, experiments, and the observations by later reviewers and collators.

The field studies of Schmidt (1920, 1923) and Heuts (1947a) are often cited as providing significant evidence for a salinity influence on vertebral number. Apparently Schmidt (1920, 1923) was the first to attempt an experimental approach to the question of salinity influencing vertebral number in fishes. Earlier Schmidt (1918) had sampled populations of the live-bearer, *Zoarces viviparus*, throughout northern Europe to correlate number of vertebrae developing with salinities of different areas. He concluded that vertebral number is not determined exclusively by the environment and the importance of salinity, especially as an influencing factor, was "greatly overestimated". Schmidt (1920) transplanted mother fish (*Zoarces viviparus*) of two different populations to live boxes in an embanked area and reared their young under the same environmental conditions; he also studied the young of mothers of the same population under different environmental conditions. He concluded that racial characteristics in a population of fish are influenced primarily by hereditary factors, but to a certain extent, are modified by environmental conditions. In the same paper he reported a correlation concerning vertebral counts and salinities in each of two fjords from the lower end to the upper. As salinity decreased, the average total number of vertebrae decreased. He did not present any temperature data and he cautioned (pp. 187–88) that any conclusion about salinity being responsible for differences in average vertebral number in the samples was unjustifiable[1]. Schmidt (1923) reported the same work with additional data and noted that although some environmental factor was influential, it could not be identified from his work.

Heuts (1947a) found a sharp bimodality for vertebral number in Belgium populations of stickleback, *Gasterosteus aculeatus*. Populations with a higher mean number of vertebrae occurred in the eastern part of the country in fresh water and populations with a lower mean vertebral number inhabited the sea during their growth period. Heuts emphasized (p. 36) that his data were inconclusive; he thought the results could be attributed to hereditary differences or to environmental factors but from his data he considered it to be impossible to identity the environmental factor[2]. Further, he stressed that some earlier works had indicated that increased numbers of vertebrae were associated with increasing salinities but in his studies the correlation was the opposite.

Relatively little experimental work has been done and only Hempel and Blaxter (1961a, 1961b) and Ali (1962) obtained results that permitted a conclusion. In Atlantic herring, *Clupea harengus*, vertebrae can only be seen relatively late in larval life at a total length of 24–30 mm. Because mortalities are high in experiments, few larvae survive long enough to develop vertebrae. But myotomes appear earlier than vertebrae and early workers thought the myotome count might be related to the vertebral count. Blaxter (1957) found this correlation to exist and concluded that myotome counts were applicable to vertebral counts. In a preliminary report Hempel and Blaxter (1961a) found a positive correlation between myotome counts and salinity. The same experiment was reported in more detail later (Hempel and Blaxter, 1961b).

Ali (1962) fertilized ova of *Oryzias latipes* in fresh water and later moved one of two 50 egg lots to water of salinity 25·9‰. Embryos reared in the sal water developed a statistically significant higher mean number of vertebrae than those reared in fresh water He concluded that salinity induced an alteration in metabolism to affect the vertebral number.

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[1] "Among the conditions which are best elucidated the salinity of the water exhibits the most characteristic picture. As will be seen from Figure 2 this factor shows a gradation which accurately corresponds with the gradation in the average number of vertebrae. To conclude from that fact that this character is directl determined by the salinity or by a factor actin parallel to it – which several investigators have been inclined to do – is however not justifiable..."

[2] "The general result of this analysis is that both, th differences between the groups as a whole and be tween population means really exist. That is to say that the fact of finding low means in the *trachura semiarmata* population is not attribuable [*sic*] to chance distribution, as it occurs by individual varia bility in any population; the same can be said fo the populations within each group. These last differ ences however we are not able to relate to any factor hereditary or external, given the observations as the are."

In an attempt to study experimentally the influence of temperature-salinity combinations upon number of vertebrae developing in the three spine stickleback, *Gasterosterus aculeatus*, Lindsey (1962) concluded that, 1) salinity as another variable produced too great a complexity to permit detailed description of the results, and 2) too few surviving fish precluded an analysis of the salinity-vertebrae relationship. Lindsey suggested that his work indicated a V-shaped salinity-temperature influence on vertebrae, and claimed that the findings of Heuts (1947a) supported this view.

Fonds et al (1974) fertilized ova of the garfish (*Belone*) at one temperature and salinity and later lots were transferred to different salinity-temperature combinations. At each temperature level mean vertebral numbers were slightly higher at the lower salinities but this study was inconclusive as far as salinity influence on vertebral number was concerned.

There have been several reviews or general treatments about the influence of environmental factors upon developing meristic structures in fishes. In regard to the influence of salinity upon vertebral number this part of the literature has ranged from informative to misleading.

Tåning (1952) remarked that although salinity had been supposed to play a considerable part in the variation of meristic characters, especially vertebrae, field observations had been inconclusive. He cited the investigations of Schmidt (1920) and Heuts (1947b); apparently the latter reference should have been Heuts (1947a) because only a passing reference to salinity and vertebral number is given in (1947b).

Barlow (1961) noted the strong correlation between a number of morphological characters and degree of adaptation to different salinities shown by Heuts (1947a), but later Barlow indicates the greatest weakness in Heuts' study was selective mortality because only adults were studied. Barlow mentions that Heuts (1956) later performed experiments that increased confidence in his earlier findings; it must be pointed out that Heuts presented no vertebral count data in this paper.

Kinne (1964) stated that the number of vertebrae is related to salinity conditions and reports that Hass (1937) found a reduction of vertebral number with decreasing salinity, but Hass actually reported (p. 318): "5. Die Durchschnittswerte der Wirbel- und Flossenstrahlenzahlen aller drei Arten werden von Salzgehalt nicht beeinflusst". Kinne stated that Hempel and Blaxter (1961a) noted the same vertebral trend in the herring, but then Kinne indicated that these authors were concerned with myomeres [*sic*]. Kinne reported that Hass (1936) observed more vertebrae in *Gobius microps* from shallow, brackish water regions than from greater depths with higher salinity. Kinne also referred to the field study of *Osmerus* by Havinga (1941) cited in Remane and Schlieper (1958) and here higher mean vertebral counts occurred in fresh water populations compared to brackish-water populations.

In a table showing the results of increasing a given environmental factor upon the number of different meristic structures developing in fishes Blaxter (1969) cited only Hempel and Blaxter (1961a, 1961b) and Lindsey (1962) as experimental investigations concerning salinity influence on vertebral number.

Fowler (1970) stated that "Substances dissolved in water also affect fish meristic characters, including vertebral number". He then cited the work of Hempel and Blaxter (1961a, 1961b) on myotomes, adding the statement that Forrester and Alderdice (1966) published similar data for the cod (*Gadus microcephalus*). These authors studied the influence of salinity and temperature on embryonic development of the Pacific cod. They demonstrated temperature and salinity influence upon rate of development, hatching times and size of larvae produced, but no data were presented concerning vertebral counts and these authors did not discuss the influence of salinity upon vertebral number. In his summary Fowler considers salinity to be equal in importance to temperature, to light and other kinds of radiation, and to dissolved substances such as oxygen in having an influence upon vertebral number in fishes.

Under the conditions of our experiment no salinity influence upon the number of vertebrae developing in embryos of *F. majalis* was indicated. However, certain structures (optic capsules, somites, pigment of the eyes) appearing first in those embryos reared at higher salinities suggested that differentiation proceeds faster at higher salinities.

There are some obvious shortcomings in our experiment. The values for pH (Table 1) of the water in the separate jars varied considerably, and although the influence of pH upon developing vertebral number has not been reported, it is possible that these variations could have masked a salinity affect. Measurements of dissolved oxygen were not made, but the relatively low mortalities (Table 1) suggest that the embryos did not lack oxygen for survival. Possibly, the amount of dissolved oxygen could have varied sufficiently to mask any salinity influence upon vertebral number. A more serious criticism of the experiment might consider the question of permeability of the egg membranes. Loeb (1912) and Kao et al (1954) found a permeability barrier in *Fundulus*; apparently within the first hour after fertilization permeability decreases. If the mechanism for salinity influence upon vertebral number involves the permeability of membranes to water or salts, then the greatest influence could be expected to occur during the period of greatest membrane permeability. In our experiment all ova were fertilized at the same salinity (32·9‰) and transferred during gastrulation to the different salinities for rearing. Only Hempel and Blaxter (1961a, 1961b) fertilized ova (*Clupea harengus*) in the same salinity in which eggs were to be reared. These workers counted myotomes that are closely correlated with vertebral counts and found a positive correlation with increasing salinity. In future experiments the time of greatest permeability of the egg membrane should be considered.

The results of field studies and field experiments have been contradictory; higher mean vertebral counts have been correlated with both higher and lower salinities. At best, correlations from field data can only be considered as weak indicators of any actual biological relationship between salinity influence and vertebral number in fishes. Well-designed experiments offer a better possibility for providing such information. Among the relatively few experiments performed, only two permitted conclusions. The experiments by Hempel and Blaxter (1961a, 1961b) indicated a direct relationship between mean myotome counts and increasing salinities. These authors were forced to work with myotomes because of developmental problems in *Clupea harengus*. Although myotome counts were determined to be related to vertebral counts, Blaxter (1957) found the number of myotomes developing in an *individual* always exceeded that of vertebrae by at least three and probably four. If there is any other variation in these additional myotomes and the actual vertebral count, statistical evaluations for vertebrae based upon myotome counts could be hazardous. In the other experiment Ali (1962) based his conclusion of a salinity influence on vertebral count upon only one 50 embryo sample reared in salt water.

The results of our experiment indicate no influence by salinity upon vertebral number in *F. majalis*. A review of the pertinent literature and the results of our simple experiment strongly suggest that salinity has not yet been shown to be an environmental factor influencing vertebral number in fishes. Certainly salinity cannot be considered as important as temperature, or even light, in this connexion. Indeed, it may be appropriate to raise the question "does salinity influence the number of vertebrae developing in fishes?" We suggest that until more results from experiments are available salinity should not be considered of major importance as an environmental factor influencing the number of vertebrae developing in fishes.

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Growth of shrimps, crabs and lobsters – an assessment

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Various highly significant linear correlations between the duration of the intermoult period and the growth factors at moulting on the one hand and body length, weight and successive moult number on the other are defined in decapod crustaceans. Log body weight or L^3 is linearly related to log age. The presence of such correlations describing the growth and moulting in other groups of Crustacea is discussed. The application of the various regression equations to the study of growth and life histories of commercial species is described.

Introduction

The growth of a crustacean can be described in terms of the growth factors at each moult and the durations of the successive intermoult periods; the growth factor is the percentage increase in body size at the moult. Estimates of the growth rates of many crustaceans are made by repeated sampling of the same population, measurement of the animals, and subsequent statistical analysis of length/frequency distributions. This method can be applied particularly to smaller species that occur in identifiable populations and that can be sampled in sufficient numbers. It is difficult to obtain accurate measures of growth rates in this way in species that migrate and in offshore pelagic and bathypelagic species. This method is also difficult to apply to larger species, such as the edible crabs and lobsters, where population densities are low. Individuals cannot be aged and moult or year classes are not discernible in polymodal size frequency distributions. Hancock and Edwards (1967) describe the technique of estimating growth rates in which large crustaceans are caught, measured, tagged and released to the natural environment. Later recovery of tagged animals allows estimations of growth rate. The returns from tagging experiments are frequently low. Consequently, estimates of growth rates are often derived from the cumulative results of a series of such experiments over a period of several years. This introduces variation in the data originating from differences in growth rates between different years.

This paper examines the relationships between moulting, growth and size of *Crangon crangon* (L.), *Palaemon serratus* Pennant, *Cancer magister* Dana, *C. pagurus* L., *Panulirus interruptus* (Randall), *P. homarus* (L.), *P. argus* Latreille, *Jasus lalandei* (H. Milne-Edwards), *Homarus americanus* H. Milne-Edwards and *H. vulgaris* H. Milne-Edwards. The results provide a means of obtaining better estimates of growth rates in commercial species than previously possible.

General approach

Kurata (1962) reviews various aspects of the relationships of moulting and growth to age or size of crustaceans. He develops a method of describing moulting and growth sequences throughout the life span of the animal and derives various constants defining the duration of the intermoult period and the increment of growth at moulting.

His analysis of the intermoult period is detailed and only a brief synopsis of the parts most relevant to this investigation are given here. He examines a a wide variety of crustaceans. The log of the duration of the intermoult period of individuals of a species of the same body size is linearly related to the log of the environmental temperature, the period decreasing with increasing temperature. A linear relationship exists when the intermoult period is related to the cube of body length or to body weight. The intermoult period linearly related to body length results in an exponential curve. This curve, however, is shallow. Transformation of the data on intermoult periods to $\log_e$ or $\log_{10}$ produces a linear correlation against body length; the correlation coefficients, however, of the linear equation and these two log equations are not usually significantly different from one another. The $\log_{10}$ transformation was selected for simplicity in handling.

The constants that Kurata uses to define the increments at moulting are obtained from regression equations relating post-moult length to pre-moult length in what Kurata calls a Hiatt growth diagram. The Hiatt growth diagram relates post-moult length on linear scales and was used by Hiatt (1948) in a study of the growth of the crab *Pachygrapsus crassipes* Randall. The main criticism of the Hiatt growth diagram (Mauchline, 1976a) is that it examines the growth increment at moulting as a contained measurement. The post-moult length equals the pre-moult length plus the increment and this is plotted against the pre-moult length. The increment ranges between about 3 and 10% of the body length throughout the greater part of the animals life, being larger in younger animals than in older. Consequently, successive plots of post- and pre-moult lengths on this diagram tend to conform to a straight line with a slope deviating from 1·0. Further, the fitting of a linear regression line to a Hiatt growth diagram assumes that the growth factors (increments expressed as percentage increase in body length) at the successive moults described by the line are constant. Kurata found that the growth factors changed and compromised by fitting two or more regression lines to the data. He terms the points where two regression lines meet inflexion points, and concludes that the growth factors alter at these points. He suggests that these inflexion points may be associated with the change from the larval to the juvenile phase of development or with the attainment of sexual maturity.

A much more rigorous treatment of growth at moulting is to examine the increment in length at various stages of the animals' life as a single parameter. Presentation of the increment as a growth factor, the percentage increase in body length at the moult, was adopted because use of the increment *per se* did not produce useful relationships. Linear plotting of successive growth factors against body length or successive moult numbers produced an exponential curve where data on young juvenile moults were included. Linear and log/linear regression equations were calculated and, as was the case for the relationship of intermoult period to body length, the correlation coefficients were not significantly different. The $\log_{10}$ transformation of the growth factors plotted against body length was adopted as more appropriate.

It thus becomes possible to plot two regression lines – one describing the increase of the intermoult period, the other describing the decrease of the growth factors – against increasing body length (Mauchline, 1976a). This general approach was evolved in studies of the growth and moulting of species of Euphausiacea (Mauchline, 1976b). It is based on measurements of body length rather than body weight because length is a much more convenient parameter, and more accurately measured, in studies of planktonic crustaceans. This paper examines the pertinence of this approach to the analyses of growth and moulting in larger commercial species.

Intermoult period

Available data on the durations of the intermoult periods of larger crustaceans are of variable quality. Many consist of observations on a few moulting individuals within a restricted size range. Others are derived from animals kept under experimental conditions of which the authors themselves are critical. Environmental temperature affects the duration of of the intermoult period but this does not seem, in practice, to be as important in investigations of wild populations as in those of laboratory experiments. The temperatures in the spring and early summer in temperate latitudes are low, producing longer intermoult periods, while those in the summer and early autumn are higher, producing shorter intermoult periods. These temperature changes seem to cancel each other in animals with marked seasonal growth. This is illustrated by recalculating the data of Kurata (1962) on the theoretical growth and moulting sequence of *Porcellio scaber* over a three year period. He makes adjustments in his calculations for seasonal changes in temperature but omission of these adjustments results in individuals of approximately the same body sizes, and having passed through the same number of moults, at the ends of each successive annual period of growth.

A selection from the available data is summarised in Table 1 taking into account the conditions in which the observations were made and the range of body size considered. The ranges of body size for each species are shown. The smallest range relative to the total range of size of the species, is that of *Jasus lalandei*. Forster (1970) examined moulting of *Palaemon serratus* in culture conditions using different diets; the data from his individual experiments are analysed separately.

Log intermoult period was regressed on body length and/or successive moult number and the correlation coefficients calculated. The corresponding linear regression equations and their correlation coefficients were also calculated; only the correlation coefficients are given in Table 1. All the correlation coefficients were significant with the exception of

Table 1. Regression analyses of intermoult period (in days) on a measurement of body length and/or successive moult number. TL, total length; CL, carapace length; MN, moult number; *n*, number of animals examined; *n*, number of mean values examined. The value and significance of the correlation coefficient *r* for the log-linear and linear-linear regressions are given.

Species	Independent measurement	Body length measurement range in mm	*n*	Regression constants log *y* = *bx* + *a*: *a*	*b*	Value and significance of *r*: log-linear	linear-linear	Source of original data
Crangon crangon								
Females	TL	TL 5–65	12	0·858	0·010	0·985***	0·964***	Meixner (1969)
Males	TL	TL 5–55	9	0·841	0·011	0·974***	0·950***	Meixner (1969)
Palaemon serratus	MN	TL 8–40						
Diet: Artemia			83	0·466	0·036	0·861***	0·822***	Forster (1970)
crab			63	0·457	0·034	0·894***	0·844***	Forster (1970)
shrimp			58	0·481	0·032	0·801***	0·810***	Forster (1970)
lugworm			73	0·439	0·042	0·938***	0·915***	Forster (1970)
mussel			62	0·415	0·054	0·928***	0·876***	Forster (1970)
Panulirus homarus								
Females	CL	CL 20–99	8	1·220	0·009	0·964***	0·987***	Berry (1971)
Males	CL	CL 20–90	7	1·216	0·009	0·947**	0·965**	Berry (1971)
Panulirus argus								
Females and males	CL	CL 20–90	7	1·505	0·004	0·953***	0·952***	Travis (1954)
Jasus lalandei								
Females and males	CL	CL 50–89	4	1·780	0·007	0·946	0·925	Fielder (1964)
Homanus americanus								
Males	MN	CL 4–35	9	0·930	0·051	0·964***	0·957***	Templeman (1948)
Males	CL	CL 4–35	9	1·129	0·013	0·928***	0·941***	Templeman (1948)

those for *Jasus lalandei*. There were no significant differences between the log–linear and linear–linear regressions for each species.

Hewett (1974) plots log intermoult period against body length, as measured by the cube root of body weight, and obtains a linear relationship in the lobster, *Homarus vulgaris*.

Consequently, plotting the log duration of the intermoult period, in days, against body length, in mm, or successive moult number provides a significant linear correlation in these larger decapods.

Growth factors

The same comments, applicable to the data on intermoult periods, are relevant to data on increments at moulting. Consequently, the data in Table 2 have been selected on the same basis as those in Table 1. The ranges in length of the various species examined are shown in Table 2 with a few exceptions which are defined below. Further comments on some of the data are required.

Palaemon serratus. Forster (1970) studied the growth of this prawn in culture. He obtained newly metamorphosed juveniles and maintained them individually in beakers. There was a heavy mortality following metamorphosis and he had varying success in weaning the juveniles from a larval diet o live *Artemia* to prepared foods such as mussel and crab. This is reflected in his Table 6 where the growth increments of the first three moults are consistently depressed. Five batches of prawns were fed different diets and their growth at thirteen successive moults observed. Moults 4–13 are considered here. Forster did not determine the sex o the animals.

Cancer pagurus. Edwards (1965) measured increments at moulting of tagged crabs and crabs maintained in the laboratory. The data from both sources are combined in Table 2. The crabs were tagged in 1959 and 1960 and the laboratory experiments extended over the period 1958–1962. Two-thirds of the data are derived from laboratory studies. The range o body size of the animals studied by Edwards (1965) is given in Table 2. Hancock and Edwards (1967) measured growth increments of tagged crabs with a range of carapace widths of 95–145 mm.

Panulirus interruptus. Lindberg (1955) measured increments at moulting primarily in captive lobsters but also in a few tagged individuals. He examined 37 females and 44 males but found little or no increase in size at moulting in 10 females and 18 males. These 28 individuals were, therefore, not included in the data used in Table 2.

Panulirus argus. Travis (1954) did not record the sex of the lobsters.

Jasus lalandei. Fielder (1964) did not determine the sex of the lobsters.

Homarus americanus. Templeman (1948) examined growth of lobsters in the size range quoted in Table 2. He constructed a growth curve and interpolated values in regions where he had no original data. The data given in his Table 8 are used in Table 2. The

Table 2. Regression analyses of growth factors on a measurement of body length. TL, total length; CL, carapace length; CW, carapace width; *n*, number of animals examined; ***n***, number of mean values examined. The value and significance of the correlation coefficients for the log-linear and linear-linear regressions are also given.

Species	Body length measurement range in mm	n	Regression constants $\log y = bx + a$ a	b	Value and significance of r log-linear	linear-linear	Source of original data
Crangon crangon							
Juveniles & females	TL 5– 65	**7**	1·512	−0·010	−0·907**	−0·855**	Meixner (1969)
Juveniles & males .	TL 5– 55	**6**	1·550	−0·013	−0·907*	−0·869*	Meixner (1969)
Palaemon serratus	TL 8– 40						
Diet: artemia		**10**	1·415	−0·011	−0·885***	−0·910***	Forster (1970)
crab		**10**	1·081	0·0003	0·020	0·035	Forster (1970)
shrimp		**10**	1·333	0·009	0·630	0·624	Forster (1970)
lugworm		**10**	1·208	−0·004	−0·448	−0·416	Forster (1970)
mussel		**10**	1·295	−0·006	−0·776**	−0·769**	Forster (1970)
Cancer magister							
Juveniles & females	CW 7–145	**15**	1·674	−0·004	−0·972***	−0·979***	Butler (1961)
Juveniles & males . .	CW 7–186	**28**	1·627	−0·002	−0·966***	−0·945***	Butler (1961)
Cancer pagurus							
Females..........	CW 16–145	65	1·426	−0·002	−0·519***	−0·544***	Edwards (1965)
Males	CW 30–134	63	1·375	−0·001	−0·364**	−0·403**	Edwards (1965)
Females..........	CW 90–149	47	1·765	−0·003	−0·670***	−0·623***	Hancock & Edwards (1967)
Males	CW 90–139	51	2·180	−0·007	−0·939***	−0·955***	
Panulirus interruptus							
Females..........	TL 100–400	27	1·211	−0·002	−0·712***	−0·689***	Lindberg (1955)
Males	TL 100–500	26	1·310	−0·003	−0·759***	−0·734***	Lindberg (1955)
Panulirus homarus							
Juveniles & females	CL 20– 94	**15**	1·645	−0·017	−0·967***	−0·928***	Berry (1971)
Juveniles & males .	CL 20– 94	**15**	1·528	−0·014	−0·982***	−0·931***	Berry (1971)
Panulirus argus							
Females & males . .	CL 40– 90	**5**	1·537	−0·014	−0·995***	−0·961***	Travis (1954)
Jasus lalandei							
Females & males . .	CL 45– 95	**6**	1·245	−0·009	−0·950**	−0·897**	Fielder (1964)
Homarus americanus							
Males	CL 4–106	**15**	1·517	−0·005	−0·986***	−0·964***	Templeman (1948)
Lismore:							
Females..........	CL 68– 88	**6**	1·691	−0·007	−0·800	−0·810	Wilder (1953)
Males	CL 68– 88	**6**	1·520	−0·004	−0·741	−0·756	Wilder (1953)
Grand Mannan:							
Females..........	CL 90–110	**6**	1·404	−0·002	−~~5~~0·585	−0·593	Wilder (1953)
Males	CL 90–110	**6**	1·622	−0·004	−0·856*	−0·857*	Wilder (1953)
Females..........	CL 55– 75	**6**	1·640	−0·006	−0·988***	−0·991***	Wilder (1963)
Males	CL 55– 75	**6**	1·573	−0·005	−0·966**	−0·961**	Wilder (1963)
Homarus vulgaris							
Females..........	CL 60–113	26	1·804	−0·009	−0·676***	−0·661***	Simpson (1961)
Males	CL 73–101	13	1·315	−0·003	−0·292	−0·306	Simpson (1961)
Females..........	CL 70– 90	62	1·747	−0·008	−0·445***	−0·455***	Thomas (1948)
Males	CL 75– 90	48	1·755	−0·007	−0·250	−0·278	Thomas (1948)

other ranges in body size examined are: Wilder (1953) Lismore, 68–88 mm, Grand Mannan, 90–110 mm; Wilder (1963), 55–75 mm.

Homarus vulgaris. Simpson (1961) estimated growth in tagged lobsters of carapace lengths 60–113 mm on the coast of North Wales while Thomas (1958) studied growth in lobsters of carapace length 72–90 mm off the southeast coast of Scotland.

The increment at moulting was expressed as a percentage increase in body size and so equivalent to a growth factor. Log growth factors were regressed on body length and the correlation coefficients calculated. The corresponding linear regression equations and correlation coefficients were also determined; only their correlation coefficients are shown in Table 2.

The correlation coefficients within each pair of regression analyses are not significantly different. There are 30 pairs of analyses. The log/linear coefficients are significant at the 0·1% level in 15 cases, at the 1% level in 5 cases and at the 5% level in 2 cases. There is no significant correlation in the remaining 8 cases. Three of these are in *Palaemon serratus* under culture conditions, the other 5 referring to investigations on *Homarus* species of restricted ranges of body size.

Lack of correlation in sets of data where the range of body length of the species investigated is small reflects the variation in the increments at each of the two or three moults represented. Such variation is evident in the raw data of Wilder, Simpson and Thomas and also in those of Ennis (1972) on *H. americanus* and Hepper (1967) on *H. vulgaris*. Thomas (1965) studied growth in *Nephrops norvegicus* of carapace length 20–50 mm and obtained a linear correlation between the growth factors and carapace length. A similar relationship was proposed by Bennett (1974) in studies of growth of *Cancer pagurus*.

Growth factors of *Palaemon serratus* calculated from two experiments of Forster (1970), and of male *Homarus americanus* from Templeman (1948) were correlated log/linearly and linearly with successive moult number (Table 3). The correlation coefficients for each pair of analyses were not significantly different.

Consequently, plotting the log growth factor against body length or successive moult number results in a significant linear correlation in these decapods.

Combined graph

The regression lines for log intermoult period and log growth factor on carapace length for *Homarus americanus* (Tables 1, 2) are drawn in Figure 1. Stage 4 lobsters measure about 4·5 cm in carapace

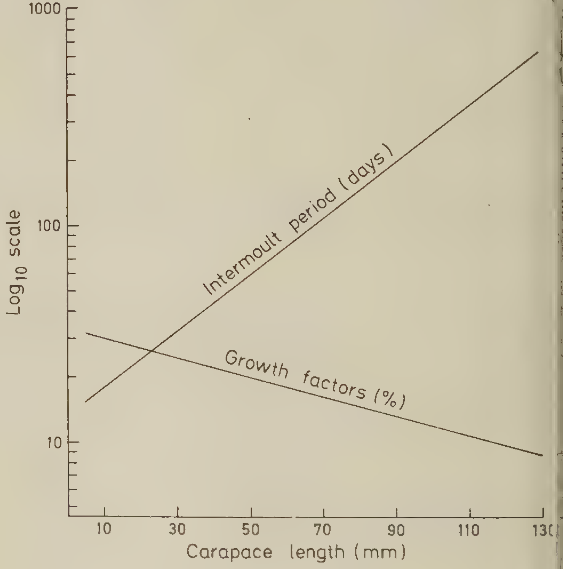

Figure 1. *Homarus americanus*. Regression lines for log intermoult period and log growth factors on carapace length. The equations are given in Tables 1 and 2.

Table 3. Regression analyses of growth factors on successive moult numbers. TL, total length; CL, carapace length. *n*, number of mean values examined. The value and significance of the correlation coefficients for the log-linear and linear-linear regressions are also given.

Species	Body length measurement	range in mm	*n*	Regression constants log $y = bx + a$ *a*	*b*	Value and significance of *r* log-linear	linear-linear	Source of original data
Palaemon serratus								
Diet: Artemia.......	TL	8– 40	10	1·416	−0·035	−0·874***	−0·901***	Forster (1970)
mussel........	TL	8– 40	10	1·306	−0·018	−0·780**	−0·773**	Forster (1970)
Homarus americanus								
Males	CL	4–106	15	1·674	−0·029	−0·988***	−0·993***	Templeman (1948

Table 4. *Homanus americanus*. A stage 4 lobster has a carapace length (CL) of 4·5 mm. The growth factor and intermoult period for the stage 4 were calculated from the equations:

$$\text{Log intermoult period} = 1{\cdot}129 + 0{\cdot}013\ \text{CL}$$
$$\text{Log growth factor} = 1{\cdot}517 - 0{\cdot}005\ \text{CL}$$

using the regression constants given in Tables 1 and 2 respectively. The carapace length of the stage 5 was then calculated by applying the growth factor to the carapace length of the stage 4 and the process repeated for each successive stage. Other columns give the corresponding values of CL^3, increment of CL^3, % increment of CL^3, age as cumulative intermoult period and adjusted age. For further explanation see text.

Stage	CL (mm)	Growth factor (%)	Intermoult period (days)	CL^3	Increment of CL^3	% increment of CL^3	Age (days)	Adjusted age (days)
4	4·50	31·37	15·37	0·91 × 10^2	1·15 × 10^2	126·37	15	15
5	5·91	30·91	16·03	2·06 × 10^2	2·58 × 10^2	125·34	31	31
6	7·74	30·34	16·91	4·64 × 10^2	5·63 × 10^2	121·34	48	48
7	10·09	29·61	18·12	1·03 × 10^3	1·21 × 10^3	117·92	66	66
8	13·08	28·71	19·79	2·24 × 10^3	2·54 × 10^3	113·40	86	86
9	16·84	27·61	22·12	4·78 × 10^3	5·15 × 10^3	107·81	108	108
10	21·49	26·31	25·36	9·93 × 10^3	1·01 × 10^4	101·41	134	134
11	27·14	24·81	29·95	2·00 × 10^4	1·89 × 10^4	94·37	164	164
12	33·87	23·14	36·53	3·89 × 10^4	3·37 × 10^4	86·76	200	380
13	41·71	21·33	46·03	7·26 × 10^4	5·71 × 10^4	78·64	246	426
14	50·61	19·45	59·82	1·30 × 10^5	9·13 × 10^4	70·40	306	486
15	60·45	17·57	79·97	2·21 × 10^5	1·38 × 10^5	62·51	386	746
16	71·07	15·74	109·3	3·59 × 10^5	1·98 × 10^5	55·06	495	855
17	82·26	14·02	152·1	5·57 × 10^5	2·68 × 10^5	48·22	647	1187
18	93·79	12·44	213·6	8·25 × 10^5	3·48 × 10^5	42·17	861	1581
19	105·46	11·03	301·3	1·17 × 10^6	4·32 × 10^5	36·87	1162	2242
20	117·09	9·77	424·5	1·61 × 10^6	5·18 × 10^5	32·27	1586	3027
21	128·53	8·68	594·7	2·12 × 10^6	6·03 × 10^5	28·38	2182	4342

length. The corresponding growth factor and intermoult period can be calculated from the equations or read from the graph. The growth factor is applied to the stage 4 lobster and the carapace length of the stage 5 obtained (Table 4). The corresponding growth factor and intermoult period of the stage 5 can then be calculated and applied to obtain the carapace length of the stage 6 lobster. These calculations were continued to stage 21.

Alternative approaches

Hewett (1974) studied the growth of *Homarus* on a weight basis. He found that the log intermoult period is linearly related to $\sqrt[3]{W}$. This relationship is analogous to that of log intermoult period related to a measurement of body length, as defined in this investigation.

He also found that the log growth increment (in g) is linearly related to log body weight (in g). This relationship was tested here. The carapace lengths calculated for the stages of *H. americanus* were transformed by cubing them (Table 4). The increment in carapace length cubed at each moult was found by the difference in carapace lengths cubed at successive moults. These were plotted on log/log scales and a linear correlation obtained, the regression constants being shown in Table 5.

Hewett also demonstrated that log body weight of the lobster is linearly related to log age. This was also tested with the data in Table 4. The ages – cumulated intermoult periods – of the different stages were calculated (Table 4). Log carapace length cubed was plotted against log age and a linear relationship found, the regression constants being in Table 5. Bennet (1974) suggested that there is a linear relationship between percentage moult increment in weight and premoult weight in the crab *Cancer pagurus*. This relationship was tested with the data in Table 4 and found to be unsatisfactory at the extremities of the range of body size.

Thus growth of crustaceans can also be studied on a weight basis as Hewett suggests. The relationships demonstrated by him on a weight basis and those demonstrated here on a length basis can be derived from each other.

Application

Kurata (1962) defined the relationship between the duration of the intermoult period and the cubic function of pre-moult body length. Hewett (1974)

Table 5. *Homarus americanus*. Regression analyses of growth transformed to relationships based on carapace length cubed (CL^3). *n*, number of mean values examined. The value and significance of the correlation coefficients of the regressions are also given. Raw data from Table 4. For further explanation see text.

Regression	*n*	Regression constants $\log y = bx + a$ *a*	*b*	Value and significance of *r*
Log increment of CL^3 on log CL^3	**18**	0·507	0·856	0·998***
Intermoult period on CL^3	**18**	18·585	0·0003	0·998***
Log CL^3 on log age	**18**	−0·943	2·316	0·986***
Log CL^3 on log adjusted age	**18**	−0·323	1·933	0·990***

could find no correlation between intermoult period and post moult weight but the regression of calculated (Table 4) intermoult periods against pre-moult carapace length cubed, gives a significant linear correlation. The regression constants are given in Table 5.

The moulting and growth sequences of a crustacean can be deduced from the minimum of data which must include accurate assessments of the intermoult period and growth increments of a few successive moults or of moults of a few animals representative of the size range of the species. They can be on a body length or weight basis and the appropriate equations calculated. The life history of the crustacean can then be postulated and tested against observations derived from studies of natural populations.

There is some growth in body length, and so probably in body weight, of crustaceans during the intermoult period. This is allowed by stretching of the integument (Mauchline, 1973) and will be accounted for as an integral part of the growth increment at the subsequent moult. The moult immediately prior to egg laying in females has no increment in body size; this moult has to be considered at the appropriate points in the life history of the females.

The suppression of moulting, and therefore of growth in body size, during winter periods of lower temperature affects the construction of a hypothetical sequence of growth and moulting such as shown in Table 4. The growth sequence of the lobster in Table 4 can be sub-divided to conform to a series of successive growing seasons. The growing season for most decapod crustaceans in British latitudes is probably about 6 months (180 days). This is equivalent to the growing season of *H. americanus* in the western Atlantic in the vicinity of Rhode Island (Templeman, 1948). The lobsters hatched in the spring probably overwinter in Stage 11. There would then be 180 days of no growth followed by a growing season of 180 days. The age of the Stages would have to be adjusted accordingly (Table 4). The second winter would be passed in Stage 14 or 15, the third in Stage 16 or 17. A moult will take place in females with no growth increment when the eggs are laid. Thereafter, moulting can only take place once every year or every second year. This discontinuous seasonal growth will affect the correlation between log body weight and log age. Log CL^3 was regressed on log adjusted age (Table 5) and a significant linear relationship was found. The presence or absence of winter growth cannot be detected in this relationship.

Conclusions

Various useful significant linear relationships have been demonstrated:

1. Log intermoult period (days) on a measurement of body length or on successive moult number.
2. Log growth factor (%) on a measurement of body length or on successive moult number.
3. Log of the cubic function of a measurement of body length (Log L^3) on log age (days).
4. Log intermoult period (days) on the cube root of body weight (g).
5. Log increment in weight (g) on log body weight (g).
6. Log body weight (g) on log age (days).

The relationships based on body weight can be derived from those based on body length and *vice versa*. They can be used to investigate growth in a variety of crustaceans but depend upon the absence of marked allometric growth. The relationships can be found within a series of similarly shaped larval stages. For example, plotting of log growth factors on successive moult number of the phyllosoma stages, described by Robertson (1968), of the sand lobster *Scyllarus americanus* (Smith) results in a highly significant linear correlation. The equations will describe the growth of the terrestrial isopod *Porcellio scaber*, described by Kurata (1962), and assessed by Mauchline (1976a). The relationship of log growth factors on successive moult number of the barnacle *Balanus improvisus* Darwin, using the data of Costlow and Bookhout (1957), demonstrates a significant linear relationship. These equations may not, however, apply to all crustaceans because preliminary examinations of ostracods and calanoid copepods have not demonstrated their relevance. Allometric growth, however, may be involved in the development of these animals.

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Enzyme extraction of the parasitic copepod *Mytilicola intestinalis* Steuer from mussels, *Mytilus edulis* L.

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Mytilicola intestinalis can be extracted from *Mytilus edulis* by means of the proteolytic enzyme papain which digests mussel flesh but not the chitinous cuticle of the copepod gut parasite. An effective method is to use 10–15 g papain powder per 100 ml of raw mussel flesh in 500 ml water and digest at 30° C for 48 h. Mussels can be digested most conveniently in shell after deep-freezing and thawing to induce their valves to gape. Filtered residues are then examined under a low-power binocular microscope. The technique has particular application in large-scale and intensive surveys of *Mytilicola* distribution because it is much more rapid than conventional dissection methods and can deal with very large samples (an examination rate of 190 mussels/hour was achieved in one trial survey of 8600 small mussels), thereby permitting more readily the detection of very low ($< 0{\cdot}1\,\%$) levels of infection.

Introduction

In England and Wales the Molluscan Shellfish (Control of Deposit) Orders 1965 and 1974 prohibit the deposit of mussels from areas where *Mytilicola intestinalis* is prevalent into areas free from this gut parasite. Recent surveys of *Mytilicola* in this country (Dare, 1974; and unpublished MAFF reports) showed that there was an urgent need to develop a quick but thorough method for examining very large samples (> 1000) of mussels from potentially exploitable stocks in marginal areas where *Mytilicola* is of only irregular and scarce occurrence. After considering various possibilities, Dr P. R. Walne suggested that the proteolytic enzyme papain might be used to digest mussel flesh and thus expose the chitinous and indigestible cuticles of any *Mytilicola* present within. Subsequently, G. Davies informed me that in 1960 he had made successful exploratory tests with papain during a *Mytilicola* survey at Morecambe Bay, and he kindly made his notes available. Using these notes as a basis, experiments were conducted during 1975 to assess the potential of this technique for large-scale surveys.

Methods and materials

Experiments were made using raw and cooked whole mussel meats, crushed raw mussels in shells, and gaping raw mussels in shells. Preliminary flesh digestion tests were made with Conwy mussels, and the resistance of *Mytilicola* to papain action was examined. The efficiency of the method was then tested using mussels of predetermined infection levels from the docks at Barrow-in-Furness, northwest England. Finally, a large-scale survey, using this method, was made of a bed of young mussels at Morecambe Bay in which *Mytilicola* had been present at a very low level of infection in 1974 (Dare, 1974).

All tests were made in 1 l beakers. The papain powder was stored in a refrigerator until required and was mixed with 500 ml of tap water just before the mussels or mussel meats were added. The mixture was then stirred and placed in an oven at 30°C The digested material was sieved through meshes o 2·5 mm (to remove shells), 1·05 mm (to remove large *Mytilicola*, byssus strands and finer debris) and 0·35 mm (to retain small *Mytilicola*). The materia from the two fine sieves was then placed in water on gridded perspex trays and scanned systematically with a low-power binocular microscope.

The digestion process produces a highly obnoxious and nauseating smell, and it is suggested that the oven be situated in an out-building, and that digested material is placed in formalin immediately after examination in order to neutralise the odour.

Results

(a) Resistance of *Mytilicola* to papain

Mytilicola cuticles are resistant to the action of papain. In preliminary tests four adults of 4–8 mm length, two of which carried egg-sacs, were placed in 50 ml of papain solution containing 5 g papain in 500 ml water and incubated at 30°C. After 48 h the chitinous cuticles were intact and appeared as virtually transparent skins, the body contents having been well digested. Later work showed that *Mytilicola* can withstand higher concentrations (10–15 g papain in 500 ml) for at least 72 h at 30°C.

(b) Digestion of mussel flesh

In 1960 G. Davies had recorded that raw mussel flesh was digested completely in 20 h at 32°C when using 5 g papain powder per 50 ml flesh in 500 ml of tap water. In the present study, using 10–15 g papain per 100 ml of flesh in 500 ml of water, it was found necessary to extend the digestion time to ensure total digestion of raw whole meats irrespective of source and size of mussel. Cooked meats, however, were not so thoroughly digested, the most resistant structures being the digestive gland and mantle. At concentrations of 10–15% papain: wet flesh, crushed shells and gaping mussels were cleaned entirely of flesh and the shell hinges of small (< 45 mm) mussels were weakened so that the valves readily separated during the digestion process.

(c) Efficiency of papain method in detecting *Mytilicola*

This was tested with a sample of infected mussels freshly collected from Barrow docks in February 1975. The sample comprised 80 large (50–70 mm) mussels and 100 small (40–50 mm) mussels. Of the larger mussels 40 were dissected in replicate groups of 10 and examined by the conventional macroscopic method (Dare, 1974), using a hand lens and scalpel to dissect the digestive gland and the hind gut; the *Mytilicola* were counted and then replaced in the meats for digestion. The raw meats from the other 40 large mussels were divided into batches of 10 and digested before examination. Of the 100 smaller mussels, the whole meats of 50 were removed for digestion while the other 50 mussels were crushed in shell before digestion.

The results (Table 1) show that the papain and macroscopic methods gave similar results on balance, although slightly more *Mytilicola* were found by using papain. However, most parasites were adults (2·5–7 mm length) and thus should not have been overlooked by the macroscopic method anyway. Crushed mussels (D) yielded fewer parasites than did extracted meats, suggesting that some *Mytilicola*

Table 1. Comparison of papain and conventional macroscopic methods of examination: the occurrence of *Mytilicola* at Barrow docks in February 1975.

Treatment	Mussel sample		Number of mussels infected (%)	Number of *Mytilicola* found		Average number of *Mytilicola* per mussel	
	Length (mm)	Number		Conventional method	Papain method	Conventional method	Papain method
A. Macroscopic examination, parasites replaced; whole raw meats then removed and digested in papain for microscopic examination	50–70	10	3	6	5		
	50–70	10	2	4	4		
	50–70	10	0	0	0		
	50–70	10	0	0	3		
		—	–	—	—		
		40	5 (12·5%)	10	12	0·25	0·30
B. No macroscopic examination, whole raw meats removed and digested as (A)	50–70	10			3		
	50–70	10			3		
	50–70	10			1		
	50–70	10			2		
		—			—		
		40			9		0·23
C. as (B)	40–50	50			12		0·24
D. Mussels crushed and digested in shells, with microscopic examination	40–50	50			4		0·08

were lost during sieving of the shell debris. Also, the crushing may have caused more damage to the parasites: three of four were broken in 'D' compared with only one of 12 in 'C' and two of 21 in 'A' and 'B' combined. The 37 *Mytilicola* extracted from the 180 mussels ranged from 1 mm (juvenile) to 9 mm in length.

Mytilicola can be detected at very low levels of infection. In a large-scale survey of 2000 young (15–40 mm) mussels from one Morecambe Bay bed, a single parasite was obtained (0·05% infection rate, 0·0005 parasites per mussel). At such a level *Mytilicola* would almost certainly escape detection by the conventional micro- and macro-scopic dissection methods because their time-consuming demands (see later) ordinarily restrict their application to small samples.

(d) Potential of papain method for large-scale surveys

A satisfactory method for examining very large numbers of small (< 40 mm) mussels, a size much in demand for transplanting, was found to be digestion of the raw meats within gaping shells. Overnight storage in a deep-freeze not only kills the mussels but causes them all to gape upon thawing. In another survey of a bed of 18–45 mm mussels, 400 g batches of thawed and gaping mussels – each batch comprising up to 230 animals – were placed in 1 l beakers containing 500 ml of papain solution. A standard laboratory oven was employed which could hold 18×1 l beakers and thus digest up to about 4000 mussels in one loading. The total sample examined contained an estimated 8600 mussels (from counts of weighed subsamples). This exercise showed that 190 mussels per hour were processed on average, including times for preparation of samples for digestion, filtering of digested material, and microscopic examination of residues, but excluding oven times. By comparison conventional dissection methods are slow: about 50 mussels per hour for incomplete macroscopic examination, and about 10 mussels per hour for full microscopic examination (Bolster, 1954). Thus, the papain method can be as much as 19 times quicker than a comparably detailed examination of individually dissected mussels.

Discussion

The major advantage of using papain is that very large numbers of mussels can be processed quickly, thoroughly and cheaply, thus enabling rapid assessments of *Mytilicola* distribution to be made over wide areas or very detailed examinations of more limited areas. The ability to process mussels in bulk consequently increases the chances of detecting *Mytilicola* at extremely low levels of infection. A wider application of this approach may, therefore, reveal the presence of *Mytilicola* in trace densities in some localities hitherto regarded as uninfected.

Acknowledgements

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Analyse et estimation des puissances de pêche*

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An analysis of the fishing power concepts leads to a distinction between local fishing power (at a given location), and overall fishing power. Overall fishing power takes into account the ability to detect and quickly exploit rich areas.

In order to estimate local fishing power it is necessary to compare the catches of different ships operating in neighbouring areas. Such a comparison performed on two ships will give an estimate of their relative fishing powers. The closer the two ships are, the more reliable will be the estimate. A weighting function must be used, and this function is related to the spatial heterogeneity of the fish density. Such a function is provided by the variogram as defined by Matheron (1965).

Overall fishing powers can be estimated using Robson's method (1966) where no division into spatial blocks is made: the fact that a ship is in a rich or a poor area must be related to the strategic component of its overall fishing power. A comparison between local and overall fishing powers may give a good insight of the strategic activity of the fishing fleet.

The North East Atlantic albacore (*Thunnus alalunga*) surface fishery, more precisely its French component, has been studied as an example. The variograms have been estimated and appear to give a significant description of the spatial heterogeneity of the fish density. Individual local and overall fishing powers have been estimated. These calculations give information about the relative influences of local fishing powers and strategic abilities in overall fishing powers.

If the strategic index is defined as the ratio of the overall to the local fishing power it appears that the local fishing power is generally the major component of the overall fishing power of a ship; and that the strategic component cannot be neglected as important differences occur between individual strategic indices. The first result may not be true within the Spanish fleet where some ships are unable to reach the best areas at the beginning of the fishing season.

Some explanations emerge concerning individual local fishing powers and strategic indices. Local fishing power must be related first to type of gear used (bait boats and trollers appear in the fishery), and secondly to the home port of a ship. The strategic index must be essentially related to the home port.

Some statistical inferences are possible only from the estimates of local fishing power. The differences which appear between yearly estimates of the strategic index of the same ships suggest that strong random components affect these estimates.

Matheron, G. 1965. Les variables régionalisées et leur estimation. Masson et Cie, Paris. 305 pp.
Robson, D. S. 1966. Estimation of the relative fishing power of individual ships. Res. Bull. Inter. Comm. N. W. Atlantic Fish., (3): 5–14

Introduction materiel

Depuis quelques années est apparu en dynamique des populations le besoin de données d'un type nouveau, à savoir celles issues de carnets de pêche remplis quotidiennement par les pêcheurs eux-mêmes. Ainsi le CNEXO, prenant la suite d'une initiative du Pr Postel soutient un programme de collecte de données par carnets de pêche, ceci pour la pêcherie de surface du germon Nord Atlantique. La procédure de constitution et de gestion informatique des fichiers de données a été decrite par Laurec, Bard, Dao et Branellec (1976). Mais il faut aussi développer des outils théoriques nouveaux, et c'est à la conception d'une nouvelle méthode d'analyse des puissances de pêche qu'est consacrée cette publication. La méthode décrite a été mise au point et testée sur la pêcherie de surface du germon. Les idées qu'elle utilise sont cependant aisément généralisables, à condition de disposer d'une information suffisamment détaillée, c'est-à-dire non seulement du résultat de la pêche, mais encore de la date et du lieu où les captures ont été effectuées.

On notera enfin que les réflexions, remarques ou calculs trop détaillés ont été reportés en annexe afin de ne pas interrompre le fil du discours.

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Methode

I. Le concept de puissance de pêche

La nécessité des méthodes d'évaluation des puissances de pêche n'est plus à démontrer en dynamique des populations. La finalité de telles études peut relever de deux points de vue:

soit que l'on cherche à estimer la densité* de poissons à partir des résultats de pêche de navires connus;

soit que l'on cherche à calculer l'effort global sur un stock donné exercé par une flotte composée de navires dont les puissances de pêche individuelles ne sont pas a priori identiques.

La réflexion à ce niveau montre que le concept de puissance de pêche n'est pas aussi bien défini qu'il pourrait y paraître à première vue, et que les deux aspects évoqués ci-dessus peuvent mener à des conceptions différentes. Le rapprochement avec la distinction entre intensité de pêche et effort de pêche, développée par Beverton et Holt (1957), apparaît à cet égard fructueux.

I.1. Estimation de la densité du poisson: puissance locale

Dans ce cas, la détermination des puissances de pêche a pour but d'apporter un correctif à l'information brute: le bateau i a pris N_{ik} poissons à tel endroit, le jour k, afin de remonter à la densité de poisson à cet endroit à ce jour. Dans cette optique, on ne peut comparer que des navires ayant opéré sur des densités identiques. N'entre donc pas dans la puissance de pêche ainsi estimée l'aptitude à détecter et à se rendre sur des zones plus riches. Pour employer un langage militaire les capacités stratégiques du navire ne sont pas prises en compte.

I.2. Estimation de l'effort de pêche: puissance globale

Si le but de l'étude est de quantifier par une mesure de l'effort de pêche la pression à laquelle un stock est soumis, la notion de puissance dite puissance locale développée au paragraphe précédent n'est pas entièrement satisfaisante. La capacité à fréquenter les parties les plus riches de la zone occupée par le stock n'a pas été prise en compte. Ce fait a été nettement mis en évidence par Poinsard et Le Gue (1975): peut importe en fait de savoir que tel navi disposant d'une grande puissance locale aurait caus une forte mortalité en fréquentant une aire riche s' n'a pas pu, ou pas su s'y rendre. On ne doit pa mesurer la capacité à prendre plus ou moins de poi son dans une zone de densité donnée, mais bie l'aptitude à prélever une fraction plus ou moins im portante d'un stock donné. Pour se convaincre qu la distinction introduite n'est pas une pure spécula tion de théoricien il suffit de se souvenir que rayon d'action des divers navires d'une flottille peu parfois grandement varier. Ainsi, dans la pêcher de surface du germon existe-t-il parmi les navire espagnols de nombreux thoniers de faible tonnag pour qui les parages des Açores, zones les plus rich en juin, sont hors d'atteinte. De même pour l pêcheries multispécifiques certains navires n'explo tent-ils qu'une frange pauvre de l'aire de répartitio d'une espèce, car cette zone peut être très intéressan pour une autre espèce.

Si l'on veut s'en tenir à la relation linéaire simp entre mortalité par pêche et effort de pêche, il e fondamental de ne pas sommer les puissances local mais bien les puissances globales. Il faut ten compte non seulement de ce que le stock est attaqu plus ou moins massivement, mais aussi de ce qu' est attaqué dans des conditions de plus ou moi grande vulnérabilité. Pour aller jusqu'au bout de raisonnement il faut se poser non seulement le pr blème de l'aptitude à choisir les lieux de pêche l plus favorables, mais encore à choisir les périod d'accessibilité maximale du poisson. Un navire n'e ploitera pas nécessairement un stock donné dura toute la période où il est accessible.

Le problème est légèrement plus compliqué lorsq l'on prend en compte le temps. Les captures de de navires ayant pêché en des endroits peut-être diff rents, à un même moment, donne directement u estimation de leur puissance de pêches globales. Po comparer deux navires ayant pêché à des instan différents il faudrait prendre en compte les variatio d'importance du stock au cours du temps si celles- sont sensibles. Pour faire la part des variations la taille du stock comme de l'accessibilité il faudra en fait opérer une analyse des cohortes avec u maille temporelle fine.

I.3. Effort de pêche et intensité de pêche

Beverton et Holt (1957) distinguent la notion d'eff de pêche, qui est une mesure de la pression à laque un stock est soumis, et la notion d'intensité de pêc qui est une mesure de la pression exercée sur u zone géographique donnée. On peut ainsi relier notion d'intensité de pêche à celle de puissance locale, le concept d'effort de pêche à celui de puissance de pêche globale.

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* On parlera constamment de la densité du poisson, supposant implicitement sa capturabilité constante. Si l'on désire éviter cette hypothèse on remplacera la notion de densité par celle du produit: densité x capturabilité.

Pour surenchérir sur les remarques du paragraphe précédent il est à noter que l'effort de pêche ne saurait être défini comme l'intégrale (au sens mathématique) de l'intensité de pêche, du moins si l'on désire conserver la relation linéaire simple entre effort et mortalité par pêche. Ce problême se pose avec d'autant plus d'acuité que d'une part la densité (ou l'accessibilité) du poisson présente une hétérogénéité spatiale forte, que d'autre part l'intensité de pêche n'évolue pas de la même manière sur toute la zône de pêche. Pour définir un effort de pêche à l'aide des puissances locales on peut utiliser la méthode de Honma (1974).

II. Les variations spatio-temporelles de la densite du poisson

Pour pouvoir estimer la puissance locale, il faut parvenir à éliminer l'influence des variations de la densité du poisson. Une première méthode consiste à supposer que ces variations sont régies par une fonction simple.

Ainsi Gulland (1956) ou Robson (1966) supposent l'existence de blocs spatio-temporels de densité uniforme. Ce modèle, qui peut s'avérer trop rigide dans de nombreux cas l'est spécialement pour les grands pélagiques. Stark (1971) suppose que le logarithme de la densité du poisson est un polynome en t, x et y (t, x et y désignant respectivement le temps, la latitude et la longitude). De fait, les fluctuations sont en général trop mouvementées pour qu'un polynome de degré très faible convienne. Or que le degré s'élève et le nombre de coefficients à estimer se multiple et le modèle devient inutilisable en pratique. Le plus raisonnable est alors de supposer simplement une certaine continuité à la densité. Pour préciser ce que l'on entend par continuité, on se référera à la théorie des processus aléatoires, et plus exactement à la théorie des variables aléatoires régionalisées développée par Matheron (1965). La densité du poisson peut alors être décrite par un processus tridimensionnel, les trois dimensions en cause étant le temps, la latitude et la longitude. En un endroit et à un instant donnés, la densité est une variable aléatoire, en un endroit et à un instant proches c'est une seconde variable aléatoire, non indépendante de la précédente. Si t est la date, x la latitude et y la longitude, on notera $d(t, x, y)$ la densité correspondante, $u(t, x, y)$ le logarithme de cette densité: $u(t, x, y) = \mathrm{Log}\,[d(t, x, y)]$. On doit pour obtenir un modèle réaliste supposer que le processus invoqué possède une dérive: $E[u(t, x, y)] = m(t, x, y)$, où E désigne l'espérance mathématique, et $m(t, x, y)$ la dérive évoquée: $u(t_1, x_1, y_1) - u(t_2, x_2, y_2)$ est donc une variable aléatoire d'espérance $m(t_1, x_1, y_1) - m(t_2, x_2, y_2)$. Pour simplifier dans un premier temps, on supposera que $t_1 = t_2 = t$. $u(t, x_1, y_1) - u(t, x_2, y_2)$ est alors une variable aléatoire d'espérance $m(t, x_1, y_1) - m(t, x_2, y_2)$.

Une mesure de l'hétérogénéité spatiale est fournie par: $E[u(t, x_1, y_1) - u(t, x_2, y_2)]^2$.

Lorsque les points (x_1, y_1) et (x_2, y_2) sont proches géographiquement $m(t, x_1, y_1) - m(t, x_2, y_2)$ est négligeable et $E[u(t, x_1, y_1) - u(t, x_2, y_2)]^2$ est sensiblement égal à $E[u(t, x_1, y_1) - m(t, x_1, y_1) - u(t, x_2, y_2) + m(t, x_2, y_2)]^2$. En supposant que cette quantité ne dépende que de la distance géographique z_{12} des points (x_1, y_1) et (x_2, y_2) on aboutit donc à une fonction de cette distance z_{12} qui est une mesure des hétérogénéités spatiales. Cette fonction notée vario (z) constitue ce que Matheron appelle un variogramme. L'hypothèse qui a permis d'y aboutir, que l'on baptisera hypothèse A est discutée en annexe.* Le variogramme vario (z), fonction positive ou nulle croît généralement avec la distance z, traduisant en-celà ce que l'on a appelé une certaine continuité. Cependant, il peut ne pas tendre vers zéro avec la distance z. On dit alors selon une expression empruntée aux géologues qu'un "effet de pépite" est présent. Cet effet correspond à des phénomènes de microdistribution, que l'on ne cherche pas à élucider en-dessous d'une certaine échelle.

Pour en revenir au problème de départ, si le navire i a pris N_{ik} poissons le jour k, en ayant opéré sur une densité d_i, si de plus la puissance locale de ce navire est P_i, selon le modèle classique: $\mathrm{Log}\,(N_{ik}) = \mathrm{Log}\,(d_{ik}) + \mathrm{Log}\,(P_i) + \varepsilon_{ik}$, ε_{ik} étant un résidus inexpliqué.

De même pour le navire j ce même jour:

$$\mathrm{Log}\,(N_{jk}) = \mathrm{Log}\,(d_{jk}) + \mathrm{Log}\,(P_j) + \varepsilon_{jk}$$

de sorte que:

$$\begin{aligned}\mathrm{Log}\,(N_{ik}/N_{jk}) = {} & \mathrm{Log}\,(P_i/P_j) + \mathrm{Log}\,(d_{ik}) \\ & - \mathrm{Log}\,(d_{jk}) + \varepsilon_{ik} - \varepsilon_{jk}\end{aligned}$$

$\mathrm{Log}\,(N_{ik}/N_{jk})$ apparaît ainsi comme la somme de deux termes: le premier $\mathrm{Log}\,(P_i/P_j)$ est déterministe, le second $\mathrm{Log}\,(d_{ik}) - \mathrm{Log}\,(d_{jk}) + \varepsilon_{ik} - \varepsilon_{jk}$ est alétoire.

La variance de ce terme aléatoire est:

$$\mathrm{var}\,[\mathrm{Log}(d_{ik}) - \mathrm{Log}\,(d_{jk})] + \mathrm{var}\,(\varepsilon_{ik}) + \mathrm{var}\,(\varepsilon_{jk})$$

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* Les hypothèses, baptisées par des majuscules sont discutées dans l'annexe B.

On ajoute les variances, supposant donc l'indépendance des différents termes. Cette supposition constitue l'hypothèse B.

On suppose de plus que var (ε_{ik}) = var (ε_{jk}) = v. Cette hypothèse sera dite hypothèse C.

Muni de ce corps d'hypothèses on aboutit ainsi à la formule var [Log(N_{ik}/N_{jk})] = vario (z_{ijk}) + $2v$. Le terme $2v$ vient donc s'ajouter à l'effet de pépite et l'on notera: vari (z) = vario (z) + $2v$.

Il est alors possible, en disposant de Log(N_{ik}/N_{jk}) pour différents jours où les navires étaient à la même distance z, d'obtenir une estimation de vario (z) + $2v$, d'après la variance observée sur les Log(N_{ik}/N_{jk}). L'estimation sera évidemment affinée en moyennant les résultats obtenus pour les différents couples (i, j).

Pour compléter l'étude il faudrait maintenant revenir au cas général, celui où l'on compare la densité en (t_1, x_1, y_1) et en (t_2, x_2, y_2), sans que l'on ait nécessairement $t_1 = t_2$. Le phénomène devient alors plus complexe. On peut ainsi montrer dans l'exemple étudié que si: $x_1 = x_2 = x$ et $y_1 = y_2 = y$, $E[d(t_1, x, y) - d(t_2, x, y)]$ n'est pas nécessairement négligeable. Le plus sage est donc de ne chercher à comparer que des pêches simultanées.* La programmation s'en trouve, et ce serait en soi un motif suffisant, grandement simplifiée. On fera cependant allusion aux structures temporelles au paragraphe suivant: si les navires i et j ont opéré à une distance inférieure à une distance seuil en deux jours k_1 et k_2 différents, Log(N_{ik_1}/N_{jk_1}) et Log(N_{ik_2}/N_{jk_2}) seront supposés stochastiquement indépendants. Cette hypothèse (dite D) repose d'une part sur l'instabilité dans le temps des structures de faible dimension, d'autre part sur la mobilité des navires.

III. Estimation de la puissance de pêche locale

III. 1. Puissance de pêche comparée de deux navires

Lorsque deux bateaux opèrent groupés, la comparaison de leurs pêches donne une idée du rapport de leurs puissances de pêche locales. Même groupés, ils ont probablement rencontré des concentrations différentes. Cependant, moins ils seront proches et plus ces différences auront tendance à être marquées. C'est ce qui est traduit par la fonction vari (z) du paragraphe II.

Reprenant les notations de ce paragraphe, Log (N_{ik}/N_{jk}) est une estimation non biaisée de Log (P_i/P_j), de variance vari (z_{ijk}), si z_{ijk} est la distance des navires i et j le jour k. Si l'on ne retient que les jours où les deux navires étaient distants de moins de zc, zc étant suffisamment faible, les estimations Log(N_{ik}/N_{jk}) correspondant à des jours différents peuvent être considérées comme statistiquement indépendantes.

On dispose ainsi d'une série d'estimations indépendantes de Log(P_i/P_j). Une moyenne pondérée par les variances fournira donc l'estimation globale, notée P_{ij}, de Log(P_i/P_j).

$$P_{ij} = \frac{1}{M_{ij}} \sum_k w_{ijk} \operatorname{Log}(N_{ik}/N_{jk})$$

Si $M_{ij} = \sum\limits_k w_{ijk}$

avec $w_{ijk} = \dfrac{\text{vari}(0)}{\text{vari}(z_{ijk})}$ si $z_{ijk} < zc$

$w_{ijk} = 0$ si $z_{ijk} > zc$

Parmi les combinaisons linéaires des Log(N_{ik}/N_{jk}) telles que w_{ijk} soit nul si $z_{ijk} > zc$, cet estimateur est l'estimateur du maximum de vraisemblance. La notion de distance maximale a un double but: assurer que c'est bien la puissance locale qui est estimée (cf. § 1–4); garantir l'indépendance des divers estimateurs journaliers.

III. 2. Puissances de pêche par rapport à un ensemble de référence

III. 2.1. L'ensemble de référence. A l'issue du paragraphe III 1. on dispose d'une matrice de P_{ij} qui sont les estimations des Log(P_i/P_j). Il est évident que de toute façon les Log(P_i) calculés d'après ces P_{ij} seraient définis à une constante additive près, puisque seules importent les quantités Log(P_i) − Log(P_j). Une condition supplémentaire est donc nécessaire pour parvenir à un système unique de Log(P_i). La solution la plus simple consiste à choisir un navire i_0 comme standard, et à fixer ainsi arbitrairement sa puissance à 1. Cette procédure comporte un danger, car comme tous les résultats de pêche ceux du navire de référence comportent une part aléatoire, composante qui va affecter l'estimation de toutes les autres puissances. Il est par conséquent plus prudent d'imposer une condition du type: $\sum\limits_i u_i \cdot \operatorname{Log}(P_i) = 0$.

Les u_i sont des nombres positifs ou nuls, l'ensemble des navires i tels que u_i soit non nul constitue l'ensemble de référence. Ce peut être la flottille au complet si par exemple $u_i = 1$ pour tout i. Ce sont alors les variations des Log(P_i) par rapport à leur moyenne qui sont étudiées.

Le danger évoqué précédemment n'est pas supprimé. Il est cependant grandement réduit: une moyenne est moins soumise aux fluctuations aléatoires que chacun des termes qui la composent.

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* Sur l'exemple étudié, et il en va certainement de même pour beaucoup d'autres, d'un jour sur l'autre la densité et peut-être surtout l'accèssibilité du poisson, varient notablement.

III. 2.2. *Une méthode d'estimation des puissances de pêche individuelles.* On notera désormais $lp_i = \text{Log}(P_i)$. On dispose donc à ce niveau de l'étude d'une matrice de P_{ij}, estimations de $lp_i - lp_j$. De plus une condition linéaire supplémentaire a été choisie. Le calcul montre aisément que la variance de p_{ij} est $\text{vari}(0) \times 1/M_{ij}$ avec comme il a été dit $M_{ij} = \sum_k w_{ijk}$.

L'idée la plus simple consiste donc à minimiser la quantité:

$$\sum_{i,j} M_{ij}[(lp_i - lp_j) - p_{ij}]^2$$

En développant les calculs on aboutit au système: $\sum_j cl_{ij} lp_j = al_i \; i = 1, Nb$ si Nb est le nombre de navires étudiés, avec $cl_{ij} = M_{ij}$ pour $i \neq j$

$$cl_{ii} = -\sum_{j \neq i} M_{ij}$$

et

$$al_i = \sum_{j \neq i} M_{ij} \times p_{ij}.$$

S'ajoute à ce système linéaire qui, tel quel comporte une infinité de solutions, la condition: $\sum_i u_i lp_i = 0$.

Une des équations du système de départ peut être supprimée et remplacée par la condition supplémentaire. Le système final s'écrit donc:

$\sum_j c_{ij} \times lp_j = a_i$ avec $c_{ij} = cl_{ij}$ sauf $i = i_0$ quelconque, et $c_{i_0 j} = u_j$, ainsi que $a_i = al_i$ sauf $a_{i0} = 0$.

Ce système de Nb équations à Nb inconnues est résoluble en général, et si l'on note b_{ij} les termes de la matrice inverse de la matrice des c_{ij} la solution sera fournie par $lp_i = \sum_j b_{ij} \times a_j$.

L'estimation des $\text{Log}(p_i)$ ainsi obtenue n'est pas l'estimation du maximum de vraisemblance. Pour obtenir celle-ci, il faudrait disposer non seulement de la variance des p_{ij}, mais de leur matrice de variance-covariance complète. La taille de cette matrice est cependant telle qu'il est sans espoir de chercher à l'utiliser dans un programme sur ordinateur, programme qui est nécessairement l'aboutissement d'une méthode de calcul.

III. 3. Variance-covariance des estimations obtenues

Le système final du paragraphe III 2.2. peut s'écrire matriciellement (les majuscules correspondent aux matrices et par exemple A est la matrice des a_{ij}). $C \times LP = A$ d'ou $LP = B \times A$ avec $B = C^{-1}$. La matrice de variance-covariance de LP est alors égale à: ${}^tB \times \text{COV A} \times B$, où ${}^tB$ désigne la transposée de B, COV A la matrice de variance-covariance du vecteur A.

Il faut donc disposer de cette matrice COV A. Comme $a_i = al_i$ pour tout i sauf pour $i = i_0$ car $a_{i0} = 0$, le problème est résolu si la matrice de variance-covariance des al_i est connue.

$$al_i = \sum_{j \neq i, k} w_{ijk} \, \text{Log}(N_{ik}/N_{jk}).$$

Du fait de l'hypothèse d'indépendance des Log (N_{ik}/N_{jk}) pour différents k, lorsque les comparaisons correspondant à des distances trop grandes sont éliminées, la covariance entre al_{i1} et al_{i2} est donnée par:

$$\sum_{k, j1 \neq i1, j2 \neq i2} w_{i1j1k} \, w_{i2j2k}$$

$$\text{cov}[\text{Log}(N_{i1k}/N_{j1k}), \text{Log}(N_{i2k}/N_{j2k})]$$

Il suffit donc de connaître les covariances

$$\text{cov}[\text{Log}(N_{i1k}/N_{j1k}), \text{Log}(N_{i2k}/\text{N}_{j2k})].$$

Le calcul de ces valeurs, quelque peu douloureux a été reporté dans l'annexe C.

III. 4. Inférences statistiques

Il apparaît légitime de supposer le vecteur A distribué de façon multinormale. En effet, il est formé par la somme de contributions journalières, contributions stochastiquement indépendantes: on est donc en droit d'invoquer le théorème central limite multivariable démontré entre autres par Anderson (1958).

Supposer que A est distribué de façon multinormale équivaut à supposer que LP l'est. Sous cette hypothèse, il devient possible de bâtir des intervalles de confiance pour les $\text{Log}(P_i)$ et partant pour les P_i. Il est cependant bien connu qu'une estimation non biaisée des $\text{Log}(P_i)$ ne conduit pas à une estimation non biaisée des P_i. Il est alors possible d'appliquer la correction de Laurent (1963). Mais il importe de garder à l'esprit que si l'on travaille essentiellement sur les logarithmes, tant des captures que des puissances, le plus sage est de conserver l'estimateur non biaisé des $\text{Log}(P_i)$ [car en retour à un estimateur non biaisé des P_i correspond un estimateur biaisé des $\text{Log}(P_i)$].

Enfin l'hypothèse de multinormalité, et l'estimation de la matrice de variance-covariance permettent le test d'hypothèses linéaires: on peut tester que la moyenne, au besoin pondérée, des logarithmes des puissances des navires d'une certaine catégorie est ou non supérieure à la moyenne des puissances dans un autre groupe. On peut de même calculer la variance d'une telle moyenne et en déduire des intervalles de confiance.

IV. Estimation de la puissance de pêche globale

Dans le paragraphe II il a été considéré que lorsque deux navires opéraient groupés, le fait qu'ils aient rencontré des densités plus ou moins grandes de poisson, relevait du simple hasard. Si cela est vrai quelle que soit la distance des deux navires, il n'y a pas lieu de faire la distinction entre puissance de pêche *in situ* et puissance de pêche globale. Il ne peut y avoir de capacités stratégiques car nulle stratégie n'est possible. S'il y a vraiment des zones, plus riches et si certains navires ont plus que d'autres la capacité de les détecter et de s'y rendre, la distinction s'impose.

On a vu dans le paragraphe précédent comment estimer la puissance de pêche locale. Pour estimer la puissance de pêche globale le plus simple est alors d'utiliser la méthode de régression de Robson (1966). Cependant, on ne procèdera pas à un découpage par blocs spatiaux où la densité serait supposée uniforme. Il y a un seul bloc spatial recouvrant l'ensemble de la zone de pêche, où la densité n'est surement pas uniforme. Mais le fait qu'un navire ait ou non pu se trouver sur des zones riches fait partie de sa puissance de pêche globale. Disposer de la puissance de pêche globale et de la puissance locale permet même d'extraire de celle-là la composante "capacité stratégique". Pour en revenir à la méthode de Robson la seule division restante sera la cassure en blocs temporels.* Les aspects statistiques de la méthode ne sont cependant plus intéressants: les résidus d'un jour sur l'autre ne sont certainement pas indépendants (ils ne peuvent l'être dès que les blocs spatiaux utilisés sont larges). Reste donc un simple ajustement par les moindres carrés.

Resultats

I. Programmation

Une méthode faisant appel à des calculs lourds n'a d'utilité que si elle est programmable. La méthode de Robson (1966) dont une variante simplifiée a été préconisée pour calculer les puissances globales, a depuis longtemps été programmée, c'est un programme dû à C. L. Berude, décrit dans le rapport technique FAO n° 101 (Abramson, 1971).

La méthode exposée de calcul des puissances locales a été programmée par nos soins. En fait, deux programmes sont nécessaires, le premier détermine l'allure du variogramme ou plus exactement de la fonction notée vari (z). Le second programme effectue le calcul des puissances de pêche. Une programmation extrêmement soignée est nécessaire si l'on désire avoir accès aux variances-covariances sans sombrer dans des temps de calcul prohibitifs. Sans entrer dans une description des programmes écrits, un ordre de grandeur du temps et de la place requis peut être utile: pour 50 bateaux et une saison de 100 jours de pêche la place requise est de 20 k mots, le temps nécessaire de 1 minute 30, ceci pour le second programme, le premier occupant une place inférieure et nécessitant un temps de calcul beaucoup plus faible. Place mémoire et temps requis s'entendent sur un ordinateur CII 10070.

II. Application à la pêcherie de surface du germon (*Thunnus alalunga*) Nord Atlantique

C'est plus exactement la flottille française qui va être étudiée, car nous ne disposons pas de carnets remplis par les pêcheurs espagnols. Une étude détaillée sera publiée ultérieurement et seront simplement présentés ici quelques résultats à titre d'illustration. L'année 1972 sera plus spécialement étudiée, car c'est une année charnière dans l'histoire de la pêcherie. Les captures globales en nombre sont seules étudiées, une étude par classe d'âge étant destinée à la publication ultérieure annoncée précédemment.*

II. 1. Allure du variogramme et de la fonction vari (z)

Variogramme et fonction vari (z) ne diffèrent que d'une constante. On peut ainsi analyser l'allure du variogramme à l'aide de la fonction vari (z).

Les études ont été faites sur huit années (1967 à 1974). Les fonctions vari (z) ont été estimées séparément pour le début et la fin de chaque année d'une part, pour l'Ouest et l'Est de la zone de pêche d'autre part. Des variations apparaissent certes, mais pour chaque année une fonction vari (z) unique peut être utilisée sans erreur grave. Lorsque les distances n'excèdent pas quelques dizaines de miles cette courbe peut être assimilée à une droite, ou pour obtenir

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* La différence entre puissances de pêche globale et *in situ* relève de la capacité à choisir les zones intéressantes et à s'y rendre. De même, la différence entre puissance de pêche globale estimée comme on l'indique et celle que l'on pourrait obtenir sans découpage en blocs temporels, comparant donc simplement les rendements moyens sur une saison de pêche, relèverait de la capacité à choisir les périodes les plus intéressantes pour la pêche.

* Quant apparaissent des variations d'accessibilité avec l'age, variations susceptibles de différer d'un engin voire d'un bateau à l'autre la rigueur conduit à calculer des puissances pour une classe d'age donnée.

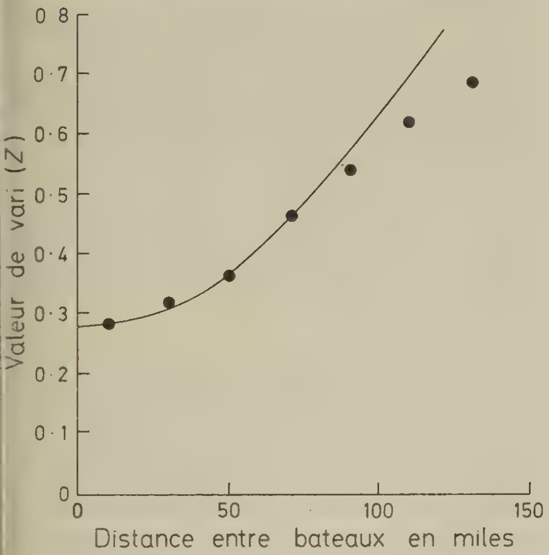

Figure 1. Estimation de la fonction vari(z).

une meilleure adéquation à un fragment de parabole à tangeante horizontale à l'origine.

La Figure 1 montre pour l'année 1972 les points estimés et l'ajustement (à l'oeil) de la parabole. Cet ajustement ne vaut qu'en deçà d'une soixantaine de miles. De toutes façons pour des distances critiques supérieures à soixante miles l'indépendance stochastique d'un jour sur l'autre des comparaisons n'est plus assurée.

L'allure du variogramme peut être utilisée pour décrire les hétérogénéités spatiales de la densité du poisson. Ainsi il apparaît qu'en des points distants de vingt ou trente miles, il n'apparaît pas d'écart sensible de densité. En revanche en étudiant le variogramme pour des distances importantes on verrait celui-ci tendre vers un palier, montrant qu'au-delà d'une distance, que l'on appelle la portée, apparaît une certaine indépendance des densités respectives. D'une année sur l'autre l'allure générale des variogrammes reste constante. La portée peut cependant changer, de même que la valeur de vari(0). On peut se demander si ces seconds changements ne sont pas dûs à une amélioration du report des données sur les carnets de pêche car vari(0) décroît régulièrement d'année en année.

La valeur à l'origine de vari(z), soit en 1972 sensiblement 0·28 montre quelle confiance on peut accorder à la capture en un jour donné d'un navire isolé comme indice de la densité de la zone fréquentée. On peut exprimer la densité logarithmique par l'espérance du logarithme des captures d'un navire de puissance locale 1, notée Log(d). Le logarithme de la pêche sur un jour d'un navire de puissance locale 1 sera alors une variable aléatoire d'espérance Log(d) et de variance 0·14 (soit 0·28/2). Si la capture indiquée est de 100 thons, l'intervalle de confiance à 5% sera (48, 208). Le calcul peut être compliqué au cas de plusieurs navires. On voit le parti que l'on peut tirer de telles considérations pour définir une stratégie de conduite des flottilles.

II. 2. Estimation des puissances locales

La distance critique utilisée est de quarante miles. De fait dès l'instant où l'on utilise une distance critique supérieure à trente miles les résultats sont stables vis-à-vis de changements de la distance critique.

Dans la pêcherie deux types de pêche sont pratiqués: la pêche à la ligne traînante (ligneurs) et la pêche à l'appât vivant (canneurs). L'ensemble de référence est constitué par les ligneurs:

$$\sum_i u_i \operatorname{Log}(p_i) = 0$$

$$u_i = 0 \text{ pour un canneur}$$

$$u_i = 1 \text{ pour un ligneur}$$

en reprenant les notations déjà utilisées.

Pour l'année 1972, quatre canneurs ont rempli des carnets de pêche. Leur puissance locale respective est 1·06, 1·76, 0·89, 1·29. La précision de ces estimations est relativement médiocre car les canneurs n'opèrent pas très souvent au voisinage des ligneurs. La moyenne géométrique des puissances locales des canneurs est 1·22. L'intervalle de confiance à 5% de cette moyenne est 1·05, 1·39. A l'imprécision sur cette moyenne s'ajoute l'incertitude quant à l'écart entre elle et la moyenne sur l'ensemble des canneurs. Cumulée sur plusieurs années, l'étude permet cependant de conclure à la plus grande puissance locale des canneurs. Sans entrer dans les détails la valeur la plus raisonnable pour la puissance locale du canneur typique est de 1·30.

A l'intérieur de la classe des ligneurs les puissances individuelles vont de 0·73 à 1·56, avec des intervalles de confiance à 5% respectivement (0·64, 0·84) et (1·34, 1·83). Entre 0·9 et 1·1 se regroupent 30% des puissances locales individuelles. Il est très difficile de relier ces puissances aux caractéristiques matérielles du thonier. Ligne d'eau, bruit et sillage sont probablement des éléments déterminants mais difficilement quantifiables ou inconnus dans l'immédiat. Un facteur prépondérant apparaît cependant, c'est le port d'attache du navire. La troisième colonne du Tableau 1 regroupe les puissances locales des thoniers de quatre ports notés A, B, C et D pour ne pas envenimer les querelles locales. L'écart systématique

Tableau 1. Logarithme des puissances globales, locales et des capacités stratégiques individuelles

Port	Log (Pg_i)	Log (Pl_i)	Log (Cs_i)
A	0·21	0·17	0·04
A	0·05	0·22	−0·17
A	0·41	0·45	−0·04
A	0·32	0·30	0·02
A	−0·03	−0·06	0·03
B	0·08	0·06	0·02
B	−0·06	−0·20	0·14
B	0·19	0·01	0·18
B	−0·07	−0·20	0·13
B	0·16	0·14	0·02
B	0·19	0·10	0·09
B	0·03	−0·07	0·10
B	0·15	0·24	−0·09
B	0·23	0·25	−0·02
B	−0·09	−0·06	−0·03
B	−0·04	−0·04	0·00
C	0·02	−0·08	0·10
C	−0·09	0·00	−0·09
C	0·04	0·10	−0·06
C	−0·07	0·00	−0·07
C	−0·15	−0·07	−0·08
C	0·08	0·19	−0·11
C	−0·09	0·03	−0·06
C	0·01	0·17	−0·16
D	−0·27	−0·34	0·07
D	−0·25	−0·14	−0·11
D	0·00	0·16	−0·16
D	−0·01	−0·21	0·20
D	−0·05	−0·16	0·11
D	−0·32	−0·28	−0·04
D	0·01	−0·23	0·24
D	0·09	0·17	−0·08
D	−0·22	−0·28	0·06
D	−0·12	−0·23	0·11
D	−0·06	−0·03	−0·03
D	−0·21	−0·21	0·00
D	−0·02	−0·21	0·19
D	−0·09	−0·04	−0·05
D	0·00	−0·16	0·16

qui semble apparaître peut être confirmé statistiquement. Là encore le problème d'inférence apparaît à deux niveaux: inférence des estimations aux valeurs réelles des puissances locales individuelles, inférence de l'échantillon des thoniers ayant rempli des carnets de pêche à la flottille complète. Le problème a priori provient de ce que les estimations individuelles sont stochastiquement liées. Cependant, leur lien est assez faible comme le montrent des coefficients de corrélation très bas. On le négligera donc pour se replacer dans le cadre statistique classique où les estimations des puissances locales individuelles sont autant de réalisations indépendantes d'une variable aléatoire (intégrant les deux niveaux évoqués plus haut).

Un test *t* sur les puissances logarithmiques montre que le port D présente une puissance locale moyenne plus faible que les autres ports, avec un seuil de significativité à 1%.

D'une année sur l'autre les puissances locales individuelles sont relativement stables. On peut améliorer la précision en effectuant une étude cumulée sur plusieurs années. D'une année sur l'autre quelques variations notables peuvent apparaître (beaucoup plus marquées dans l'ensemble que celles intervenant entre début et fin d'année). Ceci est probablement dû à des modifications techniques ou à des changements dans l'équipage.

II. 3. Estimation des puissances globales. Comparaison des deux types de puissance

Pour mieux comparer les résultats obtenus à ceux fournis par l'estimation des puissances locales, la référence à l'ensemble des ligneurs a été conservée. Par différence entre le logarithme de la puissance globale et celui de la puissance locale, on obtient ce que l'ont peut définir comme le logarithme de l'indice stratégique. Si l'on note respectivement Pg_i, Pl_i et Cs_i la puissance globale, la puissance locale et l'indice stratégique du bateau *i*: $Pg_i = Pl_i \times Cs_i$ soit $\text{Log}(Pg_i) = \text{Log}(Pl_i) + \text{Log}(Cs_i)$. La moyenne des $\text{Log}(Cs_i)$ sur l'ensemble des thoniers ligneurs sera nulle de façon évidente.

Il n'apparaît pas d'écart systématique convaincant des capacités stratégiques des ligneurs et des canneurs. Ceci dit là encore il faut souligner la faiblesse de notre échantillon, faiblesse accusée par la dispersion des puissances et capacités stratégiques individuelles.

A l'intérieur des ligneurs, les puissances globales vont de 0·73 à 1·51, avec un peu moins de la moitié des puissances entre 0·9 et 1·10. Les indices de capacité stratégique vont de 0·79 à 1·24, 60% étant comprises entre 0·9 et 1·10.

Il est à noter que la dispersion est plus forte pou les puissances locales que pour les puissances globales. La prise en compte des capacités stratégique homogénéise les puissances.

Les variations de l'indice stratégique s'éclairent là encore si l'on se réfère au port d'attache (les flottille de chaque port ont d'ailleurs tendance à se grouper). Dans le Tableau 1 ont été reportés pour les quatr ports choisis le logarithme des puissances individuelles globales et locales et le logarithme des indice stratégiques. Le Tableau 2 présente les moyenne pour chaque paramètre et chaque port. Le port D montre des puissances locales médiocres mais d bonnes capacités stratégiques. Il est à noter que dan cette pêcherie qui est souvent à la limite de la rentabilité, tout au moins pour les pêcheurs français, u thonier cumulant une mauvaise puissance locale e

Tableau 2. Moyennes port par port des logarithmes des puissances globales et locales ainsi que des capacités stratégiques

Port	Moyenne des Log (Pg_i)	Moyenne des Log (Pl_i)	Moyenne des Log (Cs_i)
A	0·20	0·22	−0·02
B	0·07	0·02	0·05
C	−0·03	0·04	−0·07
D	−0·10	−0·15	0·05

une capacité stratégique médiocre ne pourrait persévérer.

On pourrait être tenté d'étayer les raisonnements par des tests statistiques du type test *t*. Des problèmes apparaissent comme pour les puissances locales car les estimations des puissances globales individuelles sont corrélées entre elles, et cette fois de façon que l'on ne sait pas chiffrer.

Il est à noter que d'une année sur l'autre les indices tratégiques se conservent moins bien que les puisances locales. Les fluctuations ne sont cependant pas erratiques, auquel cas ceci signifierait que les capacités stratégiques seraient égales entre thoniers, t que seul le hasard ferait attribuer sur une année un indice stratégique plus ou moins grand à un avire. En effet par exemple le port C présente chaque nnée un indice stratégique logarithmique moyen égatif.

Pour préciser l'influence relative de la puissance ocale et de l'indice stratégique on peut s'en référer la moyenne en valeur absolue, ou à la moyenne uadratique des Log(Pl_i) et des Log(Cs_i). Dans les eux cas la puissance locale apparaît comme la omposante essentielle, sans que l'on puisse négliger indice stratégique.

Discussion

a première conclusion a trait à l'utilité du formasme des variables aléatoires régionalisées. La noon de variogramme est certainement un concept tile, et pourrait notamment être appliquée à des roblèmes d'échantillonnage.

La distinction des deux concepts de puissances de êche apparaît comme recouvrant bien une réalité ncrète sur l'exemple étudié. Cette distinction peret de calculer au mieux les puissances locales néssaires à l'établissement d'une cartographie des p.u.c. Elle permet d'autre part de mieux comrendre et d'expliquer la puissance globale en la parant en deux composantes: capacité stratégique puissance locale.

Ce fait est probablement utile dans toutes les pêcheries où l'activité de localisation des concentrations et de déplacement sur ces concentrations est importante.

La méthode proposée de calcul des puissances locales s'avère quant à elle opérationnelle. Lorsque la distinction entre les deux puissances ne s'impose pas, elle peut encore fournir une méthode d'évaluation des puissances présentant deux avantages: pondération des diverses comparaisons des captures de deux navires, cette pondération jouant en faveur des instants où deux navires sont proches; inférence statistique reposant sur une hypothèse moins naïve et brutale que celle des méthodes usuelles.

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Annexe A

Méthode simplifiée de calcul des puissances locales

La distance de deux navires a été considérée comme une donnée. On peut cependant envisager que seul le fai que la distance de deux bateaux soit inférieure ou non à une distance seuil zc soit connu, les distances inférieures à zc étant distribuées de façon aléatoire.

Ainsi $\mathrm{Log}(N_{ik}/N_{jk}) = \mathrm{Log}(Pi/P_j) + \varepsilon_{ijk}$, lorsque les bateaux i et j sont à une distance inférieure à zc. L variance de ε_{ijk}, supposée indépendante de k est estimée d'après la dispersion des différentes valeurs observées de $\mathrm{Log}(N_{ik}/N_{jk})$. Supposant que cette variance ne dépend pas de i et j on améliorera son estimation en moyennan les estimations obtenues pour les différents couples (i, j). On peut de même que pour la méthode complète présentée dans le paragraphe III supposer et vérifier que lorsque zc est faible les ε_{ijk} sont statisquement indépendants pour les différentes valeurs de k. Les calculs se simplifient alors légèrement (d'ou l'expression méthod simplifiée). En contrepartie, une certaine information est négligée puisque l'on considère que les distances inférieures à zc sont distribuées de façon aléatoire alors que l'on pourrait connaître leur valeur exacte.

La différence de point de vue des deux méthodes, celle dite complète et celle dite simplifiée mérite que l'o s'y attarde. Pour parfaire la formalisation mathématique il faudrait en fait considérer que la position des différents navires correspond à autant de variables aléatoires liées entre elles, et liées à la densité du poisson, densité elle-même aléatoire. Lorsque l'on suppose connu l'emplacement des divers navires, ou le fait que ces navire soient ou non distants de plus de zc on raisonne en termes de probabilités conditionnelles. Les divers points d vue correspondent à des probabilités conditionnées par différents événements.

En pratique, lorsque la puissance locale est mal individualisée, les capacités stratégiques jouant très vite dè que zc croît, la puissance estimée change de nature lorsque zc varie. Il peut alors être utile d'appliquer la méthode simplifiée pour diverses valeurs de zc. La méthode dite complète risque de masquer le problème par l poids fort attribué aux comparaisons effectuées les jours où les navires sont très proches.

Annexe B

Notes sur les principales hypothèses evoquées

Toute méthode de calcul suppose une formalisation mathématique et donc un certain nombre d'hypothèse qui ne sont jamais qu'imparfaitement satisfaites. Il est hors de propos de faire un examen exhaustif des poss bilités d'écart à ces hypothèses. Il est cependant nécessaire de réfléchir sur la signification réelle des postula invoqués, de s'assurer de leur réalisme et notamment d'évaluer l'impact possible d'un certain écart de la réali à la théorie.

On va donc revenir sur les hypothèses essentielles, lesquelles ont été identifiées par des lettres au cours l'exposé.

Hypothèse A

$u(t, x, y)$ étant le logarithme de la densité du poisson à l'endroit (x, y) à l'instant t, selon l'hypothèse

$Q(t, x_1, y_1, x_2, y_2) = E[u(t, x_1, y_1) - u(t, x_2, y_2)]^2$ ne dépend que de la distance z_{12} des points (x_1, y_1) (x_2, y_2).

a) Q est supposé indépendant de t.

En fait il est possible d'estimer Q en des époques différentes. C'est ce qui a été fait, les variations observées sont pas considérables à l'intérieur d'une saison de pêche dans l'exemple étudié. En revanche, les variatio d'une année sur l'autre sont plus marquées. Ceci semble d'ailleurs dû essentiellement à ce que la qualité renseignements portés sur les carnets croît d'année en année.

b) Q est supposé indépendant de l'emplacement géographique.

C'est en fait l'homogénéité des fluctuations spatiales qui est postulée. Ce fut examiné sur notre exemple.

c) Q ne dépend que de z_{12} et non de $x_1 - x_2$ et $y_1 - y_2$ séparément.

Cette fois ce n'est plus l'homogénéité qui est supposée mais l'isotropie. Là encore sur l'exemple étudié ceci a été examiné. En fait Q croît légèrement plus vite avec les écarts en latitude qu'en longitude. Il serait facile d'en tenir compte dans la programmation, mais la non isotropie évoquée est toutefois faible.

d) Q est supposé ne pas varier avec la densité moyenne du poisson.

On pourrait concevoir que Q ait tendance à être plus grand lorsque la densité moyenne croît. En fait il ne semble pas, une fois de plus sur l'exemple étudié qu'un tel phénomène soit significatif. Ce résultat est extrêmement important, il justifie en partie les méthodes choisies d'ajustement par les moindres carrés. Il serait nécessaire de choisir des pondérations plus sophistiquées dans le cas contraire.

Il est intéressant de noter que la méthode pourrait être modifiée si necessaire pour prendre en compte la dépendance de Q vis-à-vis de tel ou tel facteur. Ne le faisant pas on opère en fait avec une valeur moyenne.

Hypothèse B

Selon cette hypothèse B la variance de $\mathrm{Log}(N_{ik}/N_{jk})$ est: $\mathrm{var}[\mathrm{Log}(d_{ik}/d_{jk})] + \mathrm{var}(\varepsilon_{ik}) + \mathrm{var}(\varepsilon_{jk})$. Les variances s'ajoutent lorsqu'il n'y a pas d'interaction entre les différents termes d'une somme. L'interaction la plus plausible est celle liant les résidus aux densités: une haute densité pourrait provoquer une saturation de l'engin de pêche et donc des résidus négatifs dans les expressions du type $\mathrm{Log}(N_{ik}) = \mathrm{Log}(d_{ik}) + \mathrm{Log}(P_i) + \varepsilon_{ik}$. Ceci est concevable à la limite dans l'exemple du germon de surface en début de saison. En fait d'ailleurs c'est le modèle de base $\mathrm{Log}(N_{ik}) = \mathrm{Log}(d_{ik}) + \mathrm{Log}(\mathrm{P}_i) + \varepsilon_{ik}$ qui devient inadéquat.

Hypothèse C

L'hypothèse C conduit à supposer que la variance des résidus ne dépend pas du navire. Comme le montrera une note ultérieure consacrée à l'échantillonnage, il est possible d'obtenir une estimation grossière de la variance attachée à chaque navire. Pour la pêcherie de surface du germon il apparait ainsi que les canneurs possèdent une variance plus importante que les ligneurs, car ils sont plus inféodés au phénomènes de microstructures. Il serait possible de façon évidente de modifier la méthode de calcul des puissances locales en changeant simplement les pondérations.

Hypothèse D

En vertu de cette hypothèse $\mathrm{Log}(N_{ik}/N_{jk})$ et $\mathrm{Log}(N_{ik+1}/N_{jk+1})$ sont stochastiquement indépendants lorsqu'aux jours k et $k + 1$ les navires i et j ont opéré à une distance inférieure à une distance seuil zc. Elle suppose entre autres que $\mathrm{Log}(d_{ik}/d_{jk})$ et $\mathrm{Log}(d_{ik+1}/d_{jk+1})$ sont indépendants. Ceci est assuré par le choix d'une distance zc assez faible: les structures de faible dimension sont moins stables dans le temps que les structures vastes, de plus les navires sont capables de se déplacer d'un jour sur l'autre renforçant encore cette indépendance.

Une autre cause de non indépendance pourrait venir de ce que les puissances varient au cours du temps, avec une certaine continuité. C'est alors en fait une puissance moyenne qui serait estimée, les écarts à cette moyenne étant intégrés dans les résidus. Si les écarts en question possèdent une certaine continuité, l'indépendance dans le temps des résidus n'est plus assurée. En fait, il est possible d'estimer la puissance sur une période restreinte et donc de suivre ainsi une possible évolution. Sur l'exemple étudié il est ainsi apparu que si la puissance ne variait pas de façon significative dans l'année, d'une année sur l'autre elle pouvait évoluer considérablement pour certains navires (modifications humaines ou matérielles).

De toutes façons, cette hypothèse d'indépendance peut être vérifiée. Pour cela la corrélation entre $\mathrm{Log}(N_{ik}/N_{jk})$ et $\mathrm{Log}(N_{ik+1}/N_{jk+1})$, les distances des deux navires étant restées inférieures à zc, est estimée. Pour la pêcherie de surface du germon cette estimation montre que l'indépendance des résultats des comparaisons faites deux jours consécutifs peut être raisonnablement admise lorsque zc n'excède pas une soixantaine de miles.

Pour conclure cette annexe B il faut noter que lorsque les hypothèses évoquées sont enfreintes les conséquences sont essentiellement de deux types: les pondérations ne sont plus optimales. Elles demeurent cependant raisonnables pour peu que l'écart aux hypothèses ne prenne des dimensions aberrantes; les inférences sont rendues fragiles, notamment lorsque l'hypothèse D dite d'indépendance est loin d'être respectée.

En bref, les estimations obtenues restent raisonnables, et notamment pour l'essentiel non biaisées, les variances calculées devant être considérées comme indicatrice d'un ordre de grandeur, ou si l'on désire être prudent un majorant de la précision réelle des estimations obtenues.

Annexe C

Estimation de $\mathrm{cov}(al_{i_1}, al_{i_2})$; calcul de $\mathrm{cov}[\mathrm{Log}(N_{i_1k}/N_{j_1k}), \mathrm{Log}(N_{i_2k}/N_{j_2k})]$

Pour mener à bien ce calcul on remarquera d'abord que si l'on pose $p - s = (p - q) + (q - r) + (r - s)$ on obtient:

$$\mathrm{var}(p-s) = \mathrm{var}(p-q) + \mathrm{var}(q-r) + \mathrm{var}(r-s) + 2\mathrm{cov}(p-q, r-s) + 2\mathrm{cov}(p-q, q-r) + 2\mathrm{cov}(q-r, r-s)$$

Comme $\mathrm{var}(p - r) = \mathrm{var}(p - q) + \mathrm{var}(q - r) + 2\,\mathrm{cov}(p - q, q - r)$

et $\mathrm{var}(q - s) = \mathrm{var}(q - r) + \mathrm{var}(r - s) + 2\,\mathrm{cov}(q - r, r - s)$

on parvient à la relation dite relation (1):

$$2\,\mathrm{cov}(p - q, r - s) = \mathrm{var}(p - s) + \mathrm{var}(q - r) - \mathrm{var}(p - r) - \mathrm{var}(r - s).$$

D'après le paragraphe II

$\mathrm{var}[\mathrm{Log}(N_{ik}/N_{jk})] = \mathrm{vari}(z_{ijk})$ lorsque i est différent de j, si z_{ijk} est la distance des navires i et j le jour k. Lorsque $i = j$ bien évidemment $\mathrm{var}[\mathrm{Log}(N_{ik}/N_{jk})]$ est nulle.

On notera donc $\mathrm{var}[\mathrm{Log}(N_{ik}/N_{jk})] = l_{ij}\,\mathrm{vari}(z_{ijk})$.

Avec $l_{ij} = 1$ si $i \neq j$, $l_{ij} = 0$ si $i = j$

$$2\,\mathrm{cov}(\mathrm{Log}(N_{i_1k}/N_{j_1k}), \mathrm{Log}(N_{i_2k}/N_{j_2k})) = l_{i_1j_2}\,\mathrm{vari}(z_{i_1j_2k}) + l_{j_1i_2}\,\mathrm{vari}(z_{j_1i_2k})$$
$$- l_{i_1i_2}\,\mathrm{vari}(z_{i_1i_2k}) - l_{j_1j_2}\,\mathrm{vari}(z_{j_1j_2k})$$ d'après la relation (1).

Dans le cas où i_1, i_2, j_1, j_2 sont tous différents $\mathrm{cov}[\mathrm{Log}(N_{i_1k}/N_{j_1k}), \mathrm{Log}(N_{i_2k}/N_{j_2k})]$ dépend des distances deux à deux des quatre navires i_1, i_2, j_1, j_2

$\underline{i_1}$	$\underline{j_1}$	$\underline{i_1}$	$\underline{j_1}$
x	x	x	x
$\underline{i_2}$	$\underline{j_2}$	$\underline{j_2}$	$\underline{i_2}$
x	x	x	x
configuration 1		configuration 2	

Si i_2 est proche de i_1, j_2 de j_1, si i_1 est éloigné de j_2 et i_2 de j_1

(configuration 1) $\mathrm{vari}(z_{i_1j_2k}) + \mathrm{vari}(z_{i_2j_1k}) > \mathrm{vari}(z_{i_1i_2k}) + \mathrm{vari}(z_{j_1j_2k})$

$\mathrm{cov}[\mathrm{Log}(N_{i_1k}/N_{j_1k}), \mathrm{Log}(N_{i_2k}/N_{j_2k})]$ est alors positif.

La configuration 2 est obtenue en échangeant i_2 et j_2. Ainsi $\mathrm{cov}[\mathrm{Log}(N_{i_1k}/N_{j_1k}), \mathrm{Log}(N_{i_2k}/N_{j_2k})]$ change simplement de signe en gardant la même valeur absolue. Dans l'ensemble les configurations seront aléatoires et la valeur moyenne de $\mathrm{cov}[\mathrm{Log}(N_{i_1k}/N_{j_1k}), \mathrm{Log}(N_{i_2k}/N_{j_2k})]$ sera nulle, une configuration ayant la même probabilité que celle obtenue en échangeant i_2 et j_2.

Comme on somme sur les différentes valeurs de k on assimilera la moyenne à l'espérance et l'on négligera les termes où i_1, i_2, j_1, j_2 sont tous différents. La programmation en sera grandement simplifiée (quatre indices différents, conduisant à autant de boucles imbriquées aménent rapidement à des temps de calcul prohibitifs).

La covariance de al_{i_1} et al_{i_2} sera donc estimée par:

$$1/2 \sum_{k,\, j1 \neq i1,\, j2 \neq i2} g(i_1, j_1, i_2, j_2, k) \quad [l_{i_1 j_2} \,\text{vari}\,(z_{i_1 j_2 k}) + l_{i_2 j_1} \,\text{vari}\,(z_{i_2 j_1 k}) \\ - l_{i_1 i_2} \,\text{vari}\,(z_{i_1 i_2 k}) - l_{j_1 j_2} \,\text{vari}\,(z_{j_1 j_2 k})]$$

Avec $g(i_1, j_1, i_2, k) = w_{i_1 j_1 k}\, w_{i_2 j_2 k}\, f(i_1, j_1, i_2, j_2)$

où $f(i_1, j_1, i_2, j_2) = 0$ *si* i_1, j_1, i_2, j_2 sont tous différents

$= 1$ sinon.

Deux cas doivent alors être distingués:

a/ $i_1 \neq i_2$

En développant les calculs on aboutit à estimer cov(al_{i1}, al_{i2}) par

$$1/2 \sum_{k,\, j} \{w_{i_1 jk}\, l_{i_1 j}\, w_{i_2 jk}\, l_{i_2 j} [\text{vari}\,(z_{i_1 jk}) + \text{vari}\,(z_{i_2 jk})]\} \\ - [\text{vari}\,(z_{i_1 i_2 k})\, w_{i_1 i_2 k}\, (w_{i_2 jk} l_{i_2 j} + w_{i_1 jk} l_{i_1 j})]$$

b/ $i_1 = i_2 = i$

La variance de al_i est estimée par $\sum_{k,\, j} w^2_{ijk} \,\text{vari}\,(z_{ijk})$.

Annexe D

Remarque sur la non optimalité des estimateurs des puissances locales

Il a été noté que l'estimateur des puissances de pêche locales développé au paragraphe III n'était pas l'estimateur du maximum de vraisemblance. Celui-ci est en effet calculable en théorie, mais la programmation des formules obtenues deviendrait impossible. Il n'est cependant pas exclu de trouver un estimateur meilleur que celui proposé, dont l'inconvénient essentiel réside en ce que si un jour un bateau donné a été comparable à de nombreux autres, le résultat de la pêche de ce bateau en ce jour aura une importance peut être excessive sur l'estimation de sa puissance de pêche. En effet, en ce jour de nombreuses comparaisons du type Log(N_{ik}/N_{jk}) auront été opérées, et la méthode suggérée est en fait un ajustement des comparaisons théoriques Log(P_i/P_j) aux comparaisons observées Log(N_{ik}/N_{jk}).

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Relationship of sea surface temperature to American and European lobster landings

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Analyses of sea surface temperature and lobster landings data in which there are highly significant correlation coefficients between (1) temperature at Boothbay Harbor, Maine, USA, and Torungen, Aust Agder, Norway, from 1905 to 1974; (2) Maine landings of American lobsters and total European lobster landings from 1950 to 1972; (3) Boothbay Harbor temperature and Maine landings; and (4) Boothbay Harbor temperature and total European lobster landings during the same period, support the assumption that the cyclic increase and decline in landings of both species can be attributed to the same factors: corresponding cyclic increases and declines in temperature and, as has been demonstrated for northern New England and the Canadian maritimes, evidence of overfishing.

Introduction

Sea surface temperature data from the Northwest and Northeast Atlantic have been examined for their possible influence on the appreciable decline in landings of American (*Homarus americanus*) and European (*H. gammarus*) lobsters since the mid-1950's. From March 1905 to April 1951, sea surface temperature observations were made daily at Boothbay Harbor, Maine, USA, by National Marine Fisheries Service personnel, at 0800, 1200, and 1600 h, using a pail-dipped sample of sea water taken from the dock at the laboratory. Since May 1951 a thermograph has been employed with the bulb so located that it is always covered by a minimum of 1·5 m of water. Thermograph daily means are computed arithmetically from on-the-hour recordings. All temperature data are on file at the Department of Marine Resources Laboratory, Boothbay Harbor.

American lobster landings data have been collected by the National Marine Fisheries Service, the several states, and Environment Canada.

Sea surface temperature data from many stations of Northwestern Europe have been furnished by the ICES Hydrographer, Jens Smed, and long-term sea surface temperature records at Torungen, Norway, have been supplied by R. Ljøen and R. Saetre of the Institute of Marine Research, Bergen.

Landings of European lobsters by countries since 1950 are summarized in Table 1 of the 1975 ICES "Report of the Working Group on *Homarus* stocks," (Anon, 1975).

Methods

Dow and Trott (1956) reported on a joint biological-economic investigation of the Maine lobster fishery by the Maine Department of Marine Resources and the Department of Labor and Industry. This study demonstrated a highly significant correlation coefficient of 0·76 between annual mean sea surface temperature at Boothbay Harbor and the total annual landings of lobsters in Maine during the 23-year period 1932–1954.

Other research demonstrated the influence of sea surface temperature fluctuations in the Northwest Atlantic on the abundance and landings of American lobster (Martin, 1953; Taylor, Bigelow and Graham, 1957).

Simple linear correlations utilizing arithmetic means of sea surface temperature have been used throughout present studies.

Results

Analysis of these data indicates highly significant sea surface temperature correlations between Torungen and Boothbay Harbor, Maine, USA, during the years since 1905 when observations were first recorded at Boothbay Harbor (Welch, 1967) (Fig. 1). The average annual mean at Boothbay Harbor has been 8·3°C, while at Torungen it has been 8·6°C for the period 1905–1974. Temperatures at Boothbay

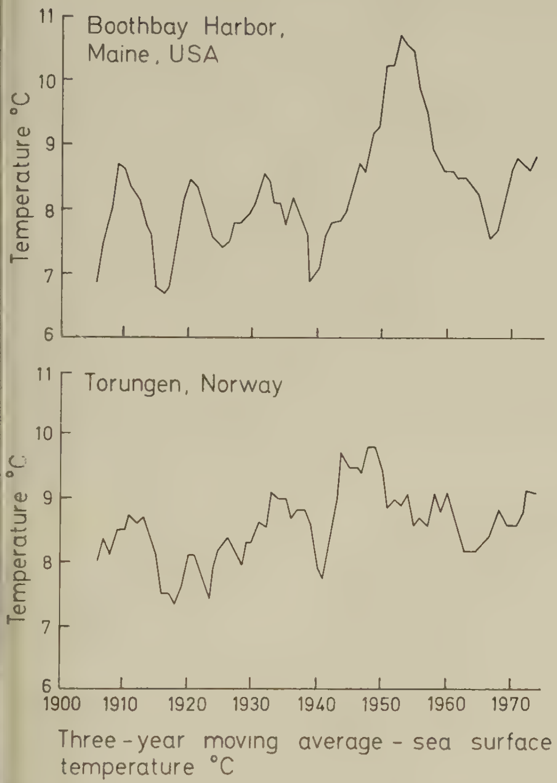

Figure 1. Three-year moving average sea-surface temperatures at Boothbay Harbor, Maine, and Torungen, Norway.

Harbor range more widely, from a minimum 6·3°C in 1917 to a high of 11·1°C in 1953, in contrast to 7·3°C annual mean from 1917 to 1919 at Torungen and a peak of 10·2°C in 1949. Although sea surface temperature correlations are highly significant between the two stations, cyclic highs and lows have not occurred at the same time (Table 1). Generally Torungen sea surface temperature lags two to four years behind Boothbay Harbor temperature.

Landings of European lobsters in Table 1 of the ICES "Report of the Working Group on *Homarus* Stocks," confirm the decline of the European lobster fishery in recent years. Similar declines in American lobster landings from New Hampshire to Newfoundland occurred during the same period.

Studies have clearly established the consistent association of sea surface temperature and inshore lobster abundance and catch fluctuations both in Maine as well as throughout the Newfoundland–New York segment of the American lobster's inshore range (Dow, 1969). While temperature appears to be the major environmental factor limiting lobster abundance, fishing effort in the Maine fishery beginning about 1850 has fluctuated with market demand.

Since the lobster is a luxury food, demand has been greatly influenced by economic conditions. During periods of high demand, fishing effort and landings have expanded to the capacity of the resource, a capacity which has fluctuated nearly two-to-one with mean annual sea surface temperature fluctuations associated with climatic cycles. A multiple correlation among catch, effort, and sea surface temperature, with 46 observations between 1905 and 1970, has an r^2 value of 0·933 with an $R^{1\cdot 23}$ value of 0·440 (Dow, Bell and Harriman, 1975).

In Maine, where nearly 30% of the total inshore North American lobster catch is made, sea surface temperature prior to the beginning of the July–June lobster year influences:

(1) The time and magnitude of moulting by sublegal lobsters to legal size. In 1959 a highly significant correlation of 0·89 between January–July sea surface temperature at Boothbay Harbor and July–August lobster landings representing 30% of the total catch for the period 1944–1958 was reported (Dow, Harriman and Scattergood, 1959); and

(2) The survival of each year class to legal size four to seven years later when it contributes an estimated 70 to 80% to Maine landings.

North of Cape Cod lobster landings increased with the 1940–1953 rise in sea surface temperature and established peak landings as sea temperatures reached optimum levels. Landings remained high throughout the maritime provinces and Maine and New Hampshire until sea surface temperature had declined below optimum. As sea surface temperature declines continued, previously higher-than-optimum temperatures were replaced by optimum conditions and landings of lobsters reached new highs in Massachusetts, Rhode Island, Connecticut, and New York, as well as in areas further south to North Carolina,

Table 1. The occurrence of high and low mean annual sea surface temperatures at Boothbay Harbor, Maine, and Torungen, Aust Agder, Norway, 1905–1974.

Boothbay Harbor		Torungen	
Year	°C	Year	°C
1910	9·0	1914	9·2
1917	6·3	1917–1919	7·3
1931	9·1	1934	9·4
1939	6·4	1941	7·6
1953	11·1	1949	10·2
1967	7·3	1963	7·7

Table 2. American lobster landings in metric tons in relation to the mean annual sea surface temperature at Boothbay Harbor, Maine, and the total fishing effort from New York to Newfoundland 1939–71. Record high landings at different locations are printed in bold type.

Year	1939	1940	1941	1942	1943	1944	1945	1946	1947	1948	1949	Change ± from Min. Max.
Mean annual sea temp. °C at Boothbay	6·4	7·0	7·8	8·1	7·4	8·0	8·4	8·5	9·2	8·2	10·1	
Location												
Newfoundland	1270	1216	1079	969	862	1040	1057	1266	1545	1686	2286	−63%
Maine	3005	3467	4054	3812	5202	6376	8677	8517	8290	7223	8742	−28%
Nova Scotia	6577	5996	6358	5772	6979	7807	8563	8491	7522	8321	9022	−24%
New Brunswick	3674	2777	2691	3195	2924	3182	3415	4213	3438	3804	4263	−51%
Prince Edward Isle	3175	2503	2674	2902	2708	3000	3673	3894	2666	2959	3104	−19%
Quebec	862	701	699	809	749	999	1101	1074	1046	1086	940	−42%
New Hampshire	81	107	–	132	**518**	311	374	–	236	182	189	−39%
Massachusetts	1057	1106	–	1022	1143	1243	1301	1489	1665	1457	1615	+82%
Rhode Island	288	169	–	196	132	106	121	163	178	174	161	+1881%
Connecticut	267	216	–	186	104	127	132	181	204	133	171	+340%
New York	106	87	–	59	82	73	54	126	178	88	125	+671%
Non-Maine Total	17357	14878	13501	15242	16201	17888	19791	20897	18678	19890	21876	
Grand Total	20362	18345	17555	19054	21403	24264	28468	29414	26968	27113	30618	
Gross Effort (Number of traps in thousands)	2452	2186	1825	1813	1794	1860	2103	2354	2504	2434	2428	

Year	1950	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	Change ± from Min./Max.
Mean annual sea temp. °C at Boothbay	9·6	10·8	10·1	11·1	10·2	10·0	9·2	9·4	8·5	8·3	8·9	
Location												
Newfoundland	2295	1960	1689	2031	2378	**2499**	2188	1904	2131	1699	2045	−63%
Maine	8324	9415	9087	10112	9818	10302	9316	**11068**	9665	10126	10889	−28%
Nova Scotia	9969	**11012**	10462	10726	10545	10408	10093	8241	8134	9553	9043	−24%
New Brunswick	5140	4792	4708	3914	3639	4100	5231	4740	4383	4233	**5404**	−51%
Prince Edward Isle	4127	3784	3799	3174	3338	3778	4400	3871	3615	3808	**4599**	−19%
Quebec	1033	1083	1050	1200	1272	1246	1657	1401	1220	1442	1611	−42%
New Hampshire	278	232	186	277	352	386	347	413	372	388	424	−39%
Massachusetts	1412	1686	1586	1712	1569	1589	1475	1500	1415	1569	1497	+82%
Rhode Island	113	96	41	55	86	101	91	118	118	185	206	+1881%
Connecticut	100	141	127	105	90	102	83	83	83	107	108	+340%
New York	52	58	117	166	114	94	93	78	85	122	106	+671%
Non-Maine Total	24519	24844	23765	23360	23383	24303	25658	22349	21556	23106	25043	
Grand Total	32843	34259	32852	33472	33201	34605	34974	33417	31221	33232	35932	
Gross Effort (Number of traps in thousands)	2483	2473	2520	2586	2926	2707	3033	3073	3053	3292	3384	

Year	1961	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971	Change ± from Min./Max.
Mean annual sea temp. °C at Boothbay	8·5	8·1	8·8	8·3	7·7	7·6	7·3	8·1	8·9	8·9	8·7	
Location												
Newfoundland	1779	1884	2038	2046	1695	1579	1415	1818	1730	1463	921	−63%
Maine	9485	10013	10344	9713	8556	9034	7479	9300	8997	8243	7964	−28%
Nova Scotia	8994	9074	9174	8670	8410	7255	6579	7166	8577	7161	8343	−24%
New Brunswick	4932	4243	3833	3293	2773	2777	2344	2699	3051	2789	2661	−51%
Prince Edward Isle	4314	3951	3346	3549	4009	3563	4065	3936	3718	3946	3717	−19%
Quebec	1549	**1918**	1737	1437	1494	1697	1501	1274	1079	1194	1108	−42%
New Hampshire	373	329	339	386	347	366	326	342	332	312	307	−39%
Massachusetts	1294	1421	1382	1703	1738	1440	1334	1567	1567	1507	**1862**	+82%
Rhode Island	176	118	76	95	175	236	235	326	404	470	**771**	+1881%
Connecticut	94	113	114	132	212	255	334	315	**365**	304	318	+340%
New York	115	79	65	112	144	209	269	285	**401**	167	388	+671%
Non-Maine Total	23620	23130	22104	21423	20997	19377	18402	19728	21224	19313	20396	
Grand Total	33105	33143	32448	31136	29553	28411	25881	29028	30221	27556	28360	
Gross Effort (Number of traps in thousands)	–	–	–	3654	–	–	–	–	3936	4962*	5634*	

* Estimated from incomplete records.

the southern terminus of the American lobster's range (Dow, 1969; Anon, 1939–1971).

During the period of sea surface temperature decline, landings continued to decrease throughout the New Hampshire to Newfoundland area at approximately the same rate as the 54% decline in European landings during the same period. From peak landings of the period to 1971, catch declined 63% in Newfoundland, 28% in Maine, 24% in Nova Scotia, 51% in New Brunswick, 19% in Prince Edward Island, 42% in Quebec, and 39% in New Hampshire, but in southern New England and New York where sea surface temperature conditions had improved for lobsters, the inshore trap catch from the period low increased 82% in Massachusetts, 1881% in Rhode Island, 340% in Connecticut, and 671% in New York (Table 2).

Discussion

Recent declines in the catch of Maine lobsters, even with optimum or near-optimum sea temperature conditions, have been shown to have been caused by overfishing (Fig. 2). This curve which approximates the catch-effort relationship described by Gulland (1968) was calculated by using three digit numbers for effort and four digit numbers for catch which were then coded for plotting.

The variable growth rate of American lobsters of the same age suggests comparison of landings in Maine and Europe on a moving average 4, 5, and 6 years following the year of egg hatching. In Maine it has been estimated that during the 1950–1972 period, from 50 to 60% of each year class would have been contributed to the catch in this three-year period.

The highly significant correlations between sea surface temperature at Boothbay Harbor and landings of American lobsters in Maine and total landings of European lobsters in all European countries are indicated by the data listed in Table 3.

There are other highly significant correlations between sea surface temperature at Boothbay Harbor and both Maine and European lobster landings as well as between Maine and European landings for the 1950–1972 period (Table 4).

Paradoxically there is generally little evidence of correlation between European sea temperatures and the catch of European lobsters except for a significant correlation between (1) sea temperatures during the April–June quarter at Torungen and the annual catch of lobsters in Norway and (2) annual sea surface temperature at Torungen and the total landings of lobster in Norway 4, 5, and 6 years later for the period 1950–1973.

On the basis of the evidence, declines in American

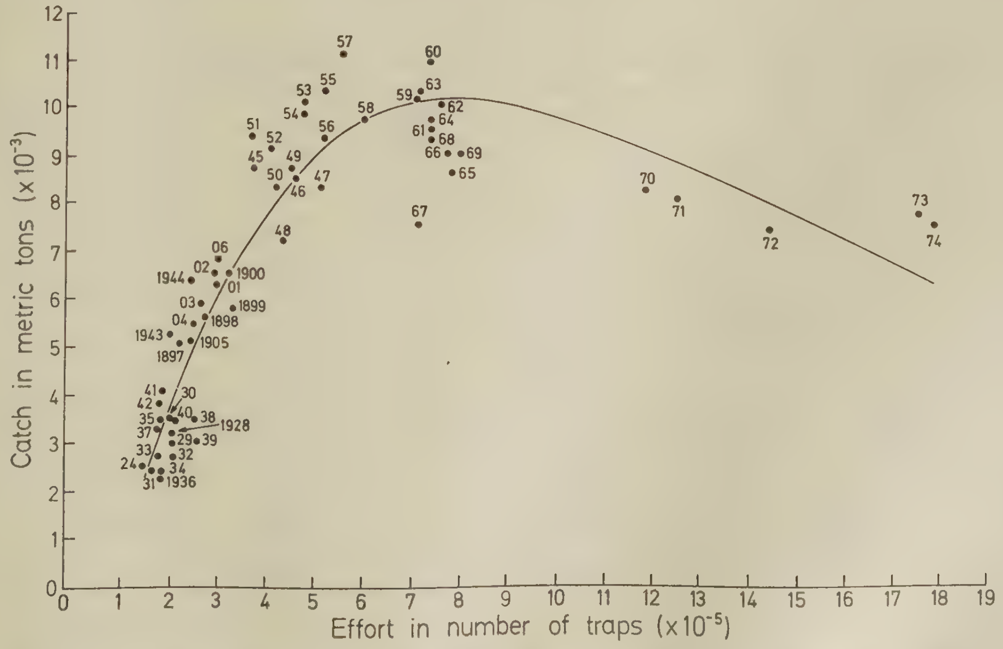

Figure 2. Catch and effort in the Maine lobster fishery 1897–1974. $\log_{10} Y = -2{\cdot}287 + 2{\cdot}893 (\log_{10} X_1) - 0{\cdot}030 (\log_{10} X_1^4)$, $\rho = 0{\cdot}999$.

Table 3. Maine annual Boothbay Harbor sea surface temperature and Maine and European lobster landings 4, 5, and 6 years later.

Year	Mean annual sea surface temperature Boothbay Harbor, Maine (°C)	Average annual landings of Maine lobsters 4, 5, and 6 years later (metric tons)	Total landings European lobsters 4, 5, and 6 years later (metric tons)
1946	8·5	8 942	8 658
1947	9·2	9 538	8 590
1948	8·2	9 672	8 522
1949	10·1	10 077	8 660
1950	9·6	9 812	8 728
1951	10·8	10 229	9 022
1952	10·1	10 016	9 307
1953	11·1	10 286	10 392
1954	10·2	10 227	10 559
1955	10·0	10 167	10 596
1956	9·2	10 129	9 204
1957	9·4	9 947	8 448
1958	8·5	10 023	7 680
1959	8·3	9 538	7 107
1960	8·9	9 101	6 962
1961	8·5	8 356	6 930
1962	8·1	8 604	7 094
1963	8·8	8 592	6 723
1964	8·3	8 847	6 420
1965	7·7	8 401	6 014
1966	7·6	7 860	5 953
Mean	9·1	9 446	8 170
r value		0·800	0·830
$r_{0\cdot01}$		0·549	0·549

and European lobster landings appear to have been caused by the same factors, less than optimum sea surface temperature and overfishing.

Acknowledgements

I thank James C. Thomas and Gary Robinson of the Department of Marine Resources for their assistance in the preparation of Figure 2; R. Ljøen and R. Sætre of the Institute of Marine Research, Bergen, and Jens Smed, ICES Hydrographer, for the data on European SST; and the General Secretary of ICES for the data on European lobster landings.

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Table 4. Sea surface temperature (SST), lobster landing correlations, and probability values.

Series	Period	Number of observations	r	$r_{0\cdot01}$	$r_{0\cdot05}$
SST 3-year moving average Boothbay Harbor, Maine *and* Torungen, Norway ..	1906–1973	68	0·55	0·311	–
SST Torungen, April–June *and* total Norway lobster catch in tons	1950–1973	24	0·45	–	0·404
SST Torungen, annual *and* total Norway lobster catch in tons 4, 5, and 6 years later	1950–1972	23	0·49	–	0·413
SST Boothbay Harbor *and* Maine lobster catch 6 years later.	1950–1972	23	0·76	0·526	–
SST Boothbay Harbor *and* European lobster catch 5 years later	1950–1972	23	0·72	0·526	–
SST Boothbay Harbor *and* European lobster catch 6 years later	1950–1972	23	0·74	0·526	–
SST Boothbay Harbor *and* total European lobster catch of 4, 5, and 6 years later	1950–1971	21	0·83	0·549	–
SST Boothbay Harbor *and* Maine lobster catch mean of 4, 5, and 6 years later.	1950–1972	21	0·80	0·549	–
SST Boothbay Harbor *and* Maine lobster catch mean of 4, 5, 6, and 7 years later. . . .	1939–1967	29	0·88	0·470	–
Maine lobster catch *and* European lobster catch	1950–1972	23	0·61	0·526	–

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J. Cons. int. Explor. Mer, 37(2): 192–193. Février 1977.

Short Notes

Estimation of mortality coefficients for exploited fish populations in which the sexes exhibit divergent growth rates

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In animal populations where the sexes have equal growth rates, changes in sex ratio have been used to estimate mortality rates, and Seber (1973) has described the mathematics underlying this method. He did not, however, deal with the related case of determining mortality rates from a single sex ratio in a fish species where the sexes have different growth rates. This paper presents a mathematical treatment of this special case, which had previously been considered by Thomas (1955) although only in a semi-quantitative manner.

For a fish stock which exhibits constant recruitment the catch, C, of fish of a given sex in the population larger than the size at first capture is given by

$$C = \frac{F}{Z} N_0 \, e^{-Mt_c}$$

where N_0 is the number present of zero age, M, F and Z are natural, fishing and total mortality coefficients respectively, t_c is the average age at first capture, and it is assumed that the maximum age, t_m, is sufficiently large that the term $\exp[-Z(t_m - t_c)]$ can be ignored (see Gulland, 1969).

It follows that the ratio of the catch of one sex to the catch of the other during the same period is given by

$$C^f/C^m = \left(\frac{F^f}{Z^f} N_0{}^f \, e^{-M^f t_c{}^f}\right) \bigg/ \left(\frac{F^m}{Z^m} N_0{}^m \, e^{-M^m t_c{}^m}\right) \quad (1)$$

where the super-scripts "f" and "m" refer to the separate sexes.

If it can be assumed that each of F^f/F^m, Z^f/Z^m, M^f/M^m and $N_0{}^f/N_0{}^m$ are unity, then Equation (1) reduces to

$$C^f/C^m = e^{-M\Delta t_c} \quad (2)$$

where $\Delta t_c = t_c{}^f - t_c{}^m$. This equation allows estimation of M if C^f/C^m and Δt_c are known.

Each of the Equations (1) and (2) can be used to provide estimates of the natural mortality coefficient, the choice of the appropriate equation being dependent on which of the other population parameters are available and how well the underlying assumptions are compatible with the fish stock under study.

If information indicates that $F^f/F^m \neq 1$, $M^f/M^m = 1$ and $N_0{}^f/N_0{}^m = 1$, and that the individual mortality coefficients for each sex are constant, then it follows from Equation (1) that

$$C^f/C^m = \frac{(Z^f - M)}{(Z^m - M)} \frac{Z^m}{Z^f} \, e^{-M\Delta t_c}$$

which after rearranging gives

$$M\Delta t_c = \log_e \left(\frac{C^m}{C^f} \frac{Z^m}{Z^f} \frac{Z^f - M}{Z^m - M}\right)$$

This equation gives a solution for M by iteration provided Z^f, Z^m, C^f/C^m and Δt_c are known.

Alternatively, if the mortality coefficients are constant but $M^f/M^m \neq 1$, $F^f/F^m = 1$, and $N_0{}^f/N_0{}^m = 1$ then it follows that Equation (1) becomes

$$C^f/C^m = \frac{Z^m}{Z^f} \, e^{(Z^m - Z^f)\, t_c{}^f - M^m \Delta t_c}$$

This equation enables the solution of M^m and hence M^f provided that Z^f, Z^m, C^f/C^m, $t_c{}^m$ and $t_c{}^f$ are known.

The sex ratio of the catch is influenced by recruitment if the sexes have markedly divergent growth rates. For example, if the recruitment is unusually high just before sampling then the recruits will contain an abnormally high proportion of the sex exhibiting the faster growth rate and hence contribute to biased estimates of M if the equations derived earlier are used. This problem can be overcome, however, by averaging the biased estimates of M for a large number of years or by using the equations derived below which hold true irrespective of whether recruitment is constant or not.

For the sex exhibiting the faster growth let l_c' be its length corresponding to the age of first capture for the other sex. The catch of fish whose lengths are greater than l_c' for this sex is then given by

$$C^{m'} = \frac{F^m}{Z^m} N_0{}^m \, e^{-Z^m(t_c{}^f - t_c{}^m) - M^m t_c{}^m}$$

From the above equation it follows that the ratio of the catch of the sex exhibiting the slower growth to the catch of the other sex above length l_c' is given by

$$C^f/C^{m'} = \left(\frac{F^f}{Z^f} N_0{}^f \, e^{-M^f t_c{}^f}\right) \Big/ \left(\frac{F^m}{Z^m} N_0{}^m \, e^{-Z^m(t_c{}^f - t_c{}^m) - M^m t_c{}^m}\right) \quad (3)$$

As previously, if it can be assumed that F^f/F^m, Z^f/Z^m, M^f/M^m and $N_0{}^f/N_0{}^m$ are unity, then Equation (3) reduces to

$$C^f/C^{m'} = e^{F\Delta t_c}$$

This equation enables the estimation of F if $C^f/C^{m'}$ and t_c are known, and hence M if Z is also known.

In a similar way to that described earlier, if $F^f/F^m \neq 1$, $M^f/M^m = 1$ and $N_0{}^f/N_0{}^m = 1$ and the mortality coefficients are constant then from Equation (3) it follows that

$$C^f/C^{m'} = \left(\frac{Z^f - M}{Z^m - M}\right) \frac{Z^m}{Z^f} \, e^{-M\Delta t_c} \, e^{Z^m \Delta t_c}$$

which after rearrangement gives

$$M\Delta t_c = Z^m \Delta t_c + \log_e \left(\frac{C^{m'}}{C^f} \frac{Z^m}{Z^f} \frac{Z^f - M}{Z^m - M}\right)$$

This equation enables an estimate of M to be obtained by iteration provided Z^f, Z^m. $C^f/C^{m'}$ and t_c are known.

Also in a similar way if the mortality coefficients are constant but $M^f/M^m \neq 1$, $F^f/F^m = 1$ and $N_0{}^f/N_0{}^m = 1$ then Equation (3) can be arranged to become

$$C^f/C^{m'} = \frac{Z^m}{Z^f} \, e^{(Z^m - Z^f)\, t_c{}^f - M^m \Delta t_c + Z^m \Delta t_c}$$

which can be used to solve for M^m and hence M^f if Z^f, Z^m, $C^f/C^{m'}$, $t_c{}^f$ and $t_c{}^m$ are known.

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J. Cons. int Explor. Mer, 37(2): 194–195. Février 1977.

Reviews

H. A. Cole (Ed.): *Petroleum and the continental shelf of western Europe. Vol. 2. Governmental Protection.* Applied Science Publishers Ltd. Barking, Essex, England, 1975. 126 pp, £ 8.00.

This book is the second of two volumes recording the proceedings of a Conference held at the Institute of Petroleum in November 1974, and called to consider problems posed by the winning of petroleum from the seabed of the shallow Continental seas of western Europe. Joint organisers of the Conference included the Institute of Petroleum, the Geological Society, the Institute of Geological Science and the Petroleum Exploration Society of Great Britain.

The volume deals with the problems of environmental protection caused by the impact of petroleum exploration, production and transport, and opens with a chapter on the role of the petroleum geologist and engineer in the maintenance of environmental quality during exploration and production operations. A note-worthy fact in this chapter is the reminder that best estimates indicate a natural input of oil to the marine environment of the order of 0·6 million metric tonnes per year over a period of perhaps 50 million years!

Further chapters, thirteen in all, deal with the engineering control problems of exploration and production drilling, the transport of oil from offshore production platforms and the oil companies' emergency planning for oil spills. The Government view on pollution problems from offshore oil production and its role in emergency planning are then examined, and this is followed by chapters giving detailed treatment of the behaviour of spilt oil at sea, the effects of exploration and production activities, including oil spills, on fisheries, effects on shore life and amenities and effects on birds. A final chapter deals with monitoring needs and the extent to which they can be met.

On the whole the proceedings of this part of the Conference give a balanced and optimistic view of the likely impact of oil from offshore production on marine environmental quality in the western European theatre. Chronic oil pollution appears to be a problem of small magnitude, unlikely to give rise to significant contamination, perhaps only detectable in the immediate vicinity of operational areas such as production platforms and offshore tanker terminals.

Some major problems will arise with the potential for conflict with other users of the maritime area, as for example the laying of pipelines through productive fishery areas, or the dumping of debris in areas likely to cause damage to gear during commercial fishing operations. The denial of some areas to fishing through the enforcement of safety or exclusion zones around drilling rigs, production platforms, pipelines and offshore terminals could also lead to friction. These types of situation have already caused some conflict and soured relations between fishermen and the oil industry on occasions. The realisation of this potential for conflict is, however, already leading to a more constructive attitude on both sides, and government is beginning to provide the legislative framework within which such accommodation can take place.

The area of greatest concern centres on oil spills, their frequency, magnitude and methods of dealing with them when they occur. No one doubts that they will occur, and that when they do they will cause damage to fisheries of a short term nature, that they can, and on occasion will, cause death and distress to seabirds and, if they drift ashore, will adversely affect amenities. The industry believes events of a major kind will be rare; government clearly needs, and will have, contingency plans but the amount o capital tied up in such contingency provisions ough to be kept in tune with the magnitude of the problem it is intended to contend with. This is a somewhat difficult balance to strike at such an early stage in offshore development in this region.

Monitoring needs are reviewed against a rigorously argued and idealised framework, and it is reluctantly concluded that the monitoring of oil contamination in all but the spill situation is as yet not practicable in terms which permit unequivocal interpretation o results. The more urgent research requirements tha need to be met in order to mount sensible monitoring activities are reviewed, and it is concluded that research leading to acceptable exposure standards fo representative target organisms, including where ap propriate man, is the most important requirement. In the absence of such standards, the routine introduction of oil from normal operations will have to be determined against best engineering standards within a 'best practicable means' framework.

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W. E. Ricker: Computation and interpretation of biological statistics of fish populations. Bull. J. Fish. Res. Bd Can. 191, 1975, 382 pp, $ 9.60.

As Dr Ricker says in his introduction, this revision of his 1958 Bulletin is not a textbook of fishery biology or a set of solutions to management problems. It is a compendium of the techniques available to assist the fishery biologist in assessing resource potential and the effect of fishing. In this it succeeds admirably, providing a wide range of examples and presented in a way which can be readily followed by fishery biologists of all shades of mathematical expertise. With this emphasis on technique the Bulletin does not attempt to set them in the context of particular resources, nor does it provide any fundamental insight into the biological processes involved. Instead it establishes clearly how to measure particular population characteristics from a set of data collected with that objective in mind. However, what has been deliberately omitted in the ecological sense is more than counterbalanced by Dr Ricker's comments on the application of the various methods. As the title indicates, this volume differs from the 1958 Bulletin by the extensive interpretation of the merits of each technique and the circumstances to which it is best suited. This, I think, is the most valuable improvement in the text aside from the inclusion of recent developments and some adjustments in notation.

The earlier Bulletin has retained its usefulness over some fifteen years: this one could stand as long again. It is produced to the customary high standards of the Fisheries Research Board of Canada and though primarily a work for reference by the specialist, browsing through the examples will give anyone interested in the technical aspects of resource assessment a useful perspective on the subject as it stands today.

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F. S. Russel and C. M. Yonge: The Seas. 4th edition, completely revised, extended and reset. Frederick Warne & Co, London. 283 pp. 48 plates (24 in colour), many line drawings. £ 6.95.

The first edition of this book originally published in 1928, was handsomely praised. In *Nature* it was described as "easily the best of the smaller books dealing with the sea" and in this Journal Michael Graham wrote that "this book should be in the library of every boy's school in the maritime countries, and it will also make a strong appeal to the growing body of laymen who are interested in science." But the earlier editions did more than that and to at least one raw university student two books in marine science stood out above the rest: Murray & Hjort's *The depths of the ocean* and Russell & Yonge's *The Seas.*

I have an affection for the original dumpy volume and its splendid frontispiece plate; and I like the new book. The 1975 edition has been reset in a somewhat larger format and contains much new material to bridge the gap of almost half a century of progress. Nevertheless there are some omissions: neither carbon-14 nor spectrophotometry are described as new techniques; the pages on production cycles make no reference to the critical depth and related concepts which were developed by Sverdrup in volume 18 of this Journal; there is no real discussion of the regulation of population numbers; density dependence is not mentioned; and radionuclides do not appear in the short section on pollution.

But if a few things have been left out, very many more have been included. This book is more of a carefully packed travelling bag than one of those voluminous trunks that are never wanted on a sea voyage: to be short of an extra pair of socks, or a couple of pocket handkerchiefs is rather a small matter.

As with the old, so with the new: it is a very good book. There is much pleasure in reading a work which communicates so much, so clearly, and with such enthusiasm. *The Seas* should be in all school and public libraries where English is read and there is an interest in the science of the sea. And it would make a good present at a very fair price.

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The stability of fish stocks

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In the common models of stock assessment, fish populations are stable and minor disturbing forces (e.g. small increments in fishing effort) cause only minor changes in the equilibrium position. Clark's (1974) conclusion, based on a "salmon" type of fish, that if there is a depensatory part of the stock/recruit relation, there will be an unstable situation, is extended to all types of population. A similar situation, in which a small increment in fishing effort can result in a collapse of the stock can also occur if (as seems to happen in some pelagic fisheries) the catchability coefficient, q, can increase with decrease in fish stock. This potential for collapse can be serious in fishery management unless there is adequate provision for monitoring the stocks, and for rapid implementation of control measures as they become necessary.

Clark, C. W. 1974. J. Cons. int. Explor. Mer, 36: 7–14.

In a recent paper Clark (1974) has drawn attention to one situation in which fish stocks may be highly unstable, and in which a small increase in fishing effort beyond a certain level can result in the complete collapse of the stock. In view of the importance of this situation to the study and management of fish stocks, it is worth examining the degree to which his conclusions hold good beyond the special case examined.

Clark considered a one generation species, harvested in a short period (i.e. short enough for natural mortality to be ignored) between recruitment and the single spawning – for example an idealized Pacific salmon. If the stock recruitment relation is given by

$$R = F(S), \quad \text{where } S = \text{spawning stock}$$

then, in a steady-state condition, a catch in numbers, C, can be taken, where

$$C = F(S) - S \tag{1}$$

Clark uses Y instead of C, but it is preferable, when the distinction may be important to reserve this symbol for yield in weight. Clark further determines the effort, f, (E in his notation) required to take this catch from the relation

$$f = \ln (F(S)/S) \tag{2}$$

which can also be deduced, in the familiar fisheries methods, from the equations

$$S = R\,\mathrm{e}^{-FT} = F(S)\mathrm{e}^{-FT} \tag{3}$$

and $F = qf$

where T = duration of the fishery season.

The two equations are equivalent if the units of effort are chosen such that $qT = 1$. Given the form of $F(S)$ Equations (1) and (2) can be readily used as parametric equations to generate the yield-effort curve, giving C as a function of f.

The more general case, of a multi-generation species, exploited over a range of ages is slightly more difficult to present, but the main features can be shown to be similar. For a given pattern of fishing, a certain set of values of fishing mortality F_t at each age will be generated, and the yield, Y, and the spawning biomass, S, will be given by the equations

$$Y = \int_0^\infty F_t w_t N_t dt \tag{4}$$

$$S = \int_0^\infty S_t w_t N_t dt \tag{5}$$

where

w_t = mean weight of fish of age t

S_t = proportion of fish age t that are spawning.

If we can ignore, for the purposes of this analysis, changes in natural mortality and growth, then Equations (4) and (5) are essentially functions of the numbers of recruits, R, and the vector $\tilde{\mathrm{F}}$ giving the fishing mortality at each age. The latter in turn is some function of the fishing effort, f, so we can write

i.e.
$$Y = R\,a(f) \tag{6}$$
$$P = R\,b(f) \tag{7}$$

The precise forms of (6) and (7) are complex, but it is clear that $b(f)$ steadily decreases with increasing f. The expression $a(f)$ is the familiar yield per recruit function. This rises from the origin, initially proportional to f. It may have a pronounced maximum if fishing starts on relatively small fish, but in many situations – including many fisheries on clupeoid stocks – the curve is relatively flat over a wide range of fishing mortalities, including the higher rates that are of primary interest in the present discussion. We will, therefore, when necessary for simplicity of discussion take $a(f)$ as constant. That is the yield per recruit in weight will be taken as approximately constant, the increase in numbers with increased fishing being balanced by a decrease in average weight.

Equation (7), and the basic stock-recruit relation $R = F(S)$ together determine the equilibrium values of S and R. These simultaneous equations are best solved graphically. The special case $f = 0$ corresponds to Figure 1 of Clark, but for any other value of f, Equation (7) determines another straight line through the origin, whose slope increases with f.

For Clark's purely compensatory case, i.e. a stock-recruit curve with no inflection, there is only one point where the line cuts the curve, and this equilibrium point steadily approaches the origin as fishing effort increases. The implications of this type of curve in which the downward-sloping left-hand part of the stock-recruit curve is within the likely range of fishing effort have been examined on a number of occasions, for example by Garrod and Jones (1974).

If the stock-recruit curve is depensatory in some parts and has a point of inflection, then the line given by Equation (7) may cut it in two points. If the slope of the stock-recruit curve at the origin is less than the slope of the line for zero effort

i.e.
$$F'(0) < 1/b(0)$$

then, corresponding to Clark's critical depensatory case, there will be two points of interaction for all values of f; otherwise there will be two equilibrium points only for those values of f above a certain level. In either case there is an upper limit to f – that given by the tangent to the stock-recruit curve which passes through the origin – above which there is no point of intersection. Any fishing effort greater than this limiting effort will lead, if maintained, to the collapse of the stock.

The case of two equilibrium points is illustrated in Figure 1. This figure can also be used, following the method of Moran (1950) to illustrate the stability of the two positions. The lines connecting one spawning stock to the subsequent recruitment (the point on the curve), to the resulting spawning stock (the point on the line) and so on, as shown by the arrows in the figure, show that the upper point [with higher stock and recruitment (S_1R_1)] is stable, and the lower one (S_2R_2) is unstable. That is, if the fishing effort (or more strictly the fishing mortality) is maintained at

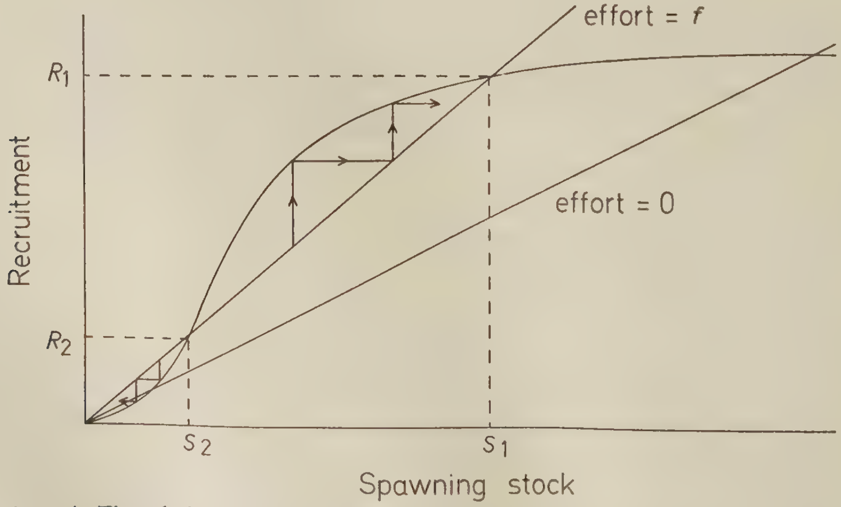

Figure 1. The relations between spawning stock and subsequent recruitment (curve), and between recruitment and resulting spawning stock under different levels of fishing effort (straight lines). The intersection R_1S_1 is a point of stable equilibrium, but R_2S_2 is unstable. Arrows denote trends in recruitment and stock if the population is disturbed from equilibrium.

the same value, then provided $S > S_2$, then the population will tend (in the absence of further disturbances) to the point S_1R_1. However, if $S < S_2$ then the stock will collapse to the origin (again in the absence of other disturbances) if the fishing effort is maintained. If $S = S_2$, then the stock will remain at this level for just so long as there is no disturbance; any disturbance will result either in a collapse, or an increase towards the stable position $S = S_1$.

These results can be used to deduce the yield/effort relation. This is not quite so easy to express in quantitative terms as in the simple case used by Clark (1974) but the quantitative results are easily seen. For low values of effort, yield increases with effort, the shape of the curve being similar to that of the left-hand side of most yield-per-recruit curves. For high values of f the yield will be roughly proportional to the recruitment. Putting these together the shape of the yield/effort curves corresponding to possible stock-recruit curves are shown in Figure 2. When there is an inflection in the latter (curve 3 of Fig. 2b), then part of the yield curve will bend back. These curves are similar to those of Clark's Figure 2, showing that his results are quite general, and not restricted to the simple case of single-age spawners exploited during a very short period immediately before spawning.

However, the equilibrium points along the backward bending part are not stable, and thus do not represent values that will occur as averages over the period if effort is maintained. If the population were to be suddenly placed at one of the equilibrium positions on this part of the curve it would be an even chance – depending on the direction of the small disturbance needed – whether it collapsed or increased towards the stable position. In the real world the population size at any time will not be exactly equal to the equilibrium value (whether stable or unstable) corresponding to the current level of fishing mortality, but will depend to a large extent on the previous history of the stock, particularly of the fishing mortality. If this has been increasing, then the stock will most likely be greater than the equilibrium value corresponding to the (high) current fishing. Therefore, the stabilizing forces will be tending to bring the population to the stable positions on the upper part of the curve, rather than causing collapse. Thus, the backward bending part is not in practice likely to be observable, as is indicated by the broken line. (The similarity of these curves to the two-dimension projections of the surfaces described by Zeeman (1976) in relation to general catastrophes suggests interesting further lines of study.)

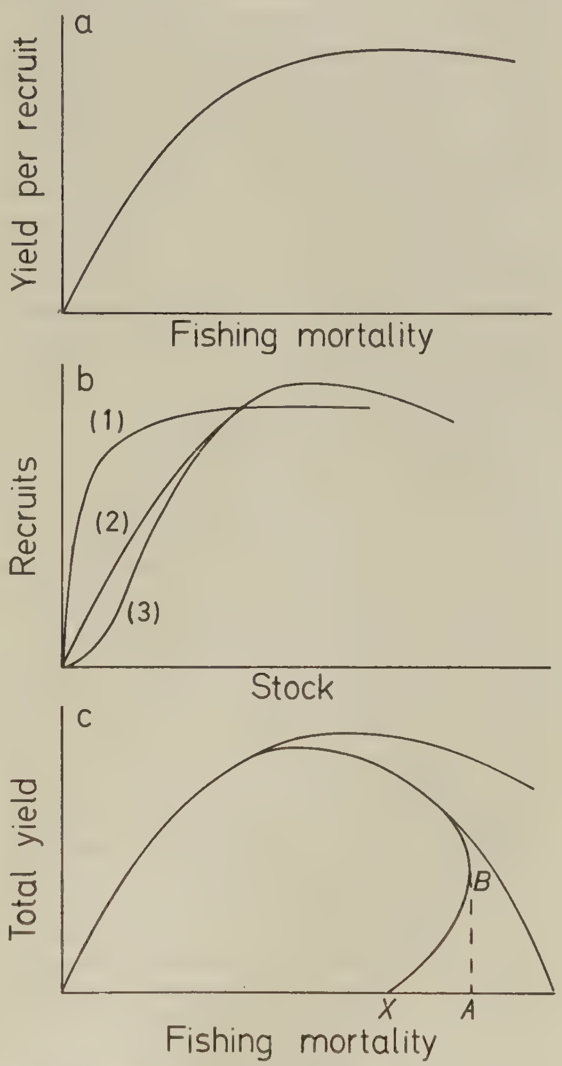

Figure 2. The effect on the yield/fishing mortality curve of different stock/recruitment relations.

a. A typical relation between fishing mortality and yield per recruit.

b. Possible stock/recruitment curves, showing a curve with almost constant recruitment (1), strong density-dependent recruitment (2), and a curve with negative density-dependence at low stocks (3).

c. The relations between total yield and fishing mortality obtained from the curves of Figures 2a and 2b.

These results, while interesting, do not appear likely to cause fishery managers undue anxiety. Clearly recruitment failures are serious, and recruitment over-fishing in the sense of Cushing (1972) is to be more carefully guarded against than growth over-fishing. However, provided the progress of the fishery along these curves can be accurately monitored there will be no problem. Even if the monitoring is somewhat ineffective, or the reaction of the manager is slow, so that the fishing mortality overshoots the point of maximum yield or even the level which can be sustained, i.e. beyond the value *AB* in Figure 2c, the result need not be permanent disaster. Provided the stock has not fallen below the critical level R_2S_2 in Figure 1, below which it collapses even in the absence of fishing (and there is little evidence that such a critical level exists for many, or indeed any, important fish stocks) a sufficient reduction in fishing mortality will lead to a recovery of the stocks. The necessary reduction will, at the worst, be one that reduces the fishing mortality below the backward-bending part of the curve, i.e. to less than *X* in Figure 2c, but a less drastic reduction to somewhat between *A* and *X* will be sufficient, provided that the population has not fallen below the (unstable) equilibrium value corresponding to that level of fishing. Further, this recovery will tend to be along the upper part of the curve in Figure 2c. This somewhat cheerful scenario does, however, suppose that action is taken in time, otherwise there may have to be a long period of low catches to rebuild the stock. An essential need is therefore adequate monitoring, and willingness and ability to act when danger signs occur.

The difficulty is that the reduction must be in fishing mortality *F*. The fisherman or fishery manager is used to thinking in terms of catch or effort, and especially they often believe that any reduction in catch or effort will result in reduction in *F*, and is a positive conservation measure. This need not be the case. The fallacy as regards catch is best illustrated by Antarctic whaling. Just prior to a critical special meeting of the International Whaling Commission in 1965, which resolved the basic conflicts between short-term and long-term interests in favour of the latter, fin whale stocks were declining very fast (at around 20–30% per year). It took much scientific argument (and the failure of the industry to achieve their quota in the 1963/64 season) to persuade the Commission and the industry that the sizes of reduction in the quota being proposed (of around 10–15%) would in fact result in *increased* fishing mortality and an accelerated decline. The catch fallacy is now well recognized, at least by scientists, though many fishermen and administrators have a somewhat natural difficulty in accepting the magnitude of reduction in *catch* that is required to achieve a reduction in mortality (and have any real conservation effect) in a situation where the stock is rapidly declining.

The effort fallacy is similar, but more insidious. The fact that a reduction in effort need not result in a reduction in mortality has proved less dangerous to date mainly because effort control has been less frequently used than catch limits. In addition to the difficulty that occurs when effort ceases to be proportional to mortality in relation to achieving a desired management policy by effort controls, the failure in proportionality can also change the whole form of the apparent yield-effort curve. Mathematically the failure in proportionality arises from changes in the catchability coefficient, *q*, in the equation

$$F = qf$$

The various ways in which the variations in *q* and their causes can be classified, have been widely discussed particularly at two ICES symposia (Gulland, 1964; Pope, 1975). These discussions mainly concerned seasonal or diurnal variations, or trends in time due to increasing power or efficiency of the fishing vessels. For the present purposes variations in *q* that are related to fish abundance – particularly when *q* increases with decreasing stock abundance – are more serious, especially at lower stock levels. The extent to which this happens depends on the gear. There seems little reason to expect the proportion of fish in the path of a trawl which are caught by it to vary appreciably with abundance. The efficiency of several types of gear (lines, traps, and possibly gill-nets) can be reduced at high fish densities by the occupation of the available space. This gear saturation is readily observed and appropriate corrections made (Gulland, 1956).

The serious problems relate to those fisheries in which searching and the success of searching is a major determinant of the catch. These include most of the fisheries on shoaling pelagic fish, particularly with purse seines, though pelagic trawling may also be affected. The question mainly relates to the measures of fishing time that are used in determining fishing effort. It is possible to break up a complete trip into a number of operations, e.g. steaming to the chosen fishing grounds, searching on these grounds, shooting and hauling the net, and returning to port. When adequate information on each of these operations is available it may be feasible to devise a measure of effort that will be proportional to the actual fishing mortality caused (Anon, 1974). Conceptually it may be easier to carry through the calculations with the immediate objective of determining an adjusted catch-per-unit-effort that provides a consistent index of abundance. For example, the number of hauls made per unit searching time (adjusted for the speed of the vessel, and searching power as evidenced by sonar or other equipment) may give an index of the number of schools per uni area. Multiplied by an index of the size of schools

.g. catch per haul corrected for the efficiency of the ear as evidenced by the size of the net, etc.) this hould provide a reasonable index of density. A urther adjustment, using some estimates of the reas of the stock may be necessary to provide an ndex of abundance.

This is fine provided sufficiently detailed informa-on on the commercial operations are available from og books. Even in the more detailed log book ystems, e.g. those of I-ATTC for tropical tunas, and n Peru for the anchoveta fishery, this may not be ompletely true. More generally the best effort in-ormation relates to numbers of landings, days at ea, or numbers of hauls. Any of these, if used to ompute effort, can result in values of q that in-rease rapidly as the stock decreases.

A number of mechanisms can cause increases in q s the stock decreases. For example, the area in-abited can shrink, maintaining the density and in-ices of catch-per-unit-effort. Often the school size ill remain the same, while the number of schools all, so that catch per haul remains steady. In-reases in q that do result in some fall in c.p.u.e. but ot as great as the actual decrease in abundance, can e caused by a greater part of the unit fishing time he trip, or the day at sea) being spent in searching. athematically these effects can be expressed as a elation $q = \alpha P^{\beta}$ where P = abundance of the fish-ble population.

It may be important to note that P, that part of e total population (from eggs to adults) which is xposed to fishing, i.e. the fishable or recruited part, ill not in general be the same as the spawning stock. any fisheries are based partly or predominantly on sh while they are immature. While the effects dis-ussed below are not directly concerned with any ecific relationship between the abundance of the dult stock and subsequent recruitment, the results ould be made more serious if reductions in adult ock did affect recruitment.

The usual basic assumption that q, the catch-bility coefficient, is constant is given by $\beta = 0$ and creases in q with decreases in stock by $\beta < 0$. or the particular case of $\beta = -1$, c.p.u.e. remains onstant despite changes in stock. Fox (in press) as found that data for the Californian sardine shery is fitted by $\beta = -0{\cdot}3$.

Fox (in press) has examined the consequence of e above relation to the usual analyses of catch d efforts data. His extension of the GENPROD odel (Pella and Tomlinson, 1969) becomes

$$-dP/dt = HP^m - KP - \alpha P^{\beta} f \cdot P$$

om which he derived the equilibrium value of ffort, in terms of the catch-per-unit-effort, U, as,

$$f = aU^b + cU^d$$

where a, b, c, and d are functions of H, K, α, β and m.

From this the other relations between effort, catch, and catch-per-unit-effort (biomass) can be readily deduced. The important conclusion, as pointed out by Fox, is that for some values of m, including the traditional Schaefer (1954) value of $m = 2$, when $\beta < 0$, this can produce a backward bending yield curve. For example Fox's Figure 8 shows the fit to the data of the Californian sardine, which in terms of nominal fishing effort has a backward bending curve like Figure 2c, even though the equivalent relation between yield and fishing mortality is the typical parabolic Schaefer curve (or the GENPROD curve for $m = 2$). The backward curvature in this case has no connection with the basic biology of the fish, but is due wholly to the difficulty of getting a proper measure of fishing effort, i.e. one proportional to fishing mortality.

The stability of the equilibrium position in the backward bending part of the curve is clearly important. There are a number of different ways in which the system could be temporarily disturbed from a equilibrium position, including changes in fishing effort, e.g. diversion to or from another stock in which conditions are temporarily better or worse, in average stock size (e.g. the entry of a good or bad year class), or in the catchability coefficient, i.e. in the fishing mortality caused by a given fishing effort, (e.g. by unusual hydrographic conditions concentrating the fish). Though they may differ in detail in their effects, it would seem that these all tend again

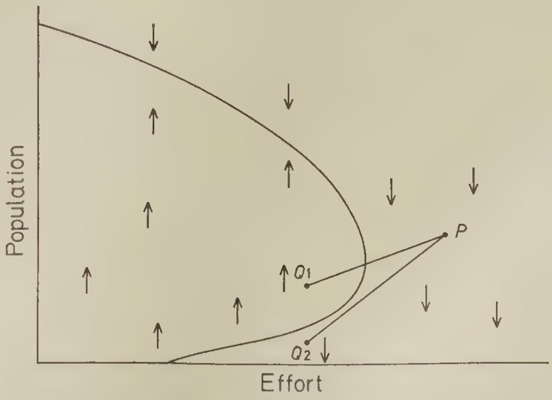

Figure 3. Possible relations between fishing effort and equilibrium population size if the catchability coefficient (q) varies with stock abundance. The arrows show the trends in population size if the population is not on the equilibrium line. Note that only the points on the upper part of the line are stable. Q_1, Q_2 denote successful and unsuccessful changes in a fishery on a too heavily fished stock originally at state P.

to make the lower, backward bending part of the curve unstable. Suppose for example the catchability increases then the fishing mortality resulting from the same nominal effort will increase, tending to further depress the stock. Conversely, if the catchability drops, then there will be some increase in population, therefore even after conditions return to normal, a drop in mortality and hence a further recovery in population. The likely stability may therefore correspond to that illustrated in Figure 3. This shows a possible equilibrium relation between population abundance and nominal fishing effort corresponding to the backward bending yield-effort curve in Figure 2c. The arrows indicate the changes in population likely to occur (other things being equal) away from the equilibrium line. They illustrate the lack of stability in the backward bending part. The figure also illustrates an important conclusion for management of fisheries in which the effort has increased beyond the level that can be maintained, e.g. to *P*. If the effort is reduced quickly enough within the sustainable range, i.e. so that there has not been much drop in population, e.g. to point Q_1 then the population will recover. However, if the cut in effort is not fast enough or far enough, e.g. to Q_2 the collapse can continue. That is, in fishery management, as in war, too little and too late can be fatal, and early but moderate action can be as effective as drastic but slow response to management needs. This in turn requires adequate response in all the links in the management chain, not least in th monitoring and scientific analysis.

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Skylab investigation of the upwelling off the northwest coast of Africa[1]

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The upwelling off the NW coast of Africa in the vicinity of Cap Blanc was studied in February–March 1974 from aircraft and in September 1973 from Skylab. The aircraft study was designed to determine the effectiveness of a differential radiometer in quantifying surface chlorophyll concentrations. Photographic images of the S190A Multispectral Camera and the S190B Earth Terrain Camera from Skylab were used to study distributional patterns of suspended material and to locate ocean colour boundaries. The thermal channel of the S192 Multispectral Scanner was used to map sea-surface temperature distributions off Cap Blanc. Correlating ocean colour changes with temperature gradients is an effective method of qualitatively estimating biological productivity in the upwelling region off Africa.

Introduction

From a practical standpoint, phytoplankton is a very important life form in the ocean, since primary productivity can be directly related to potential production of commercial fish. In upwelling regions of the world, such as off the northwest coast of Africa, wind stress produces an offshore movement of surface waters which are replaced by cooler, nutrient-rich subsurface waters. These upwelled waters are an excellent medium for the propagation of phytoplankton. Though upwelling regions comprise only about 0·1% of the ocean surface, Ryther (1969) estimates that they produce about half of the world's fish supply.

When studying plankton over large areas of the ocean, oceanographers face serious logistics problems. Since it may take several days to several weeks to cover a large study area by ship, the best that can be hoped for is a time-averaged picture of plankton distributions. The ship sampling programme may miss patches of plankton of significant interest and the concentrations may be changing rapidly over time. Since large surface areas of the ocean can be easily seen from space, the possibility of synoptically determining plankton quantities and distributions from earth orbit is extremely attractive. (Szekielda, 1973).

On 4 September 1973, the Skylab spacecraft passed directly over the Cap Blanc section of NW Africa. This report will summarize the interpretation to date of radiometeric data derived from Skylab as it pertains to plankton distributions off the African coast.

Atmospheric conditions

The NW coast of Africa can be effectively studied from space, since favourable meteorological conditions are present throughout most of the year. During winter in the northern hemisphere, a high pressure system is centred between the Canary Islands and the Azores. In summer, this system extends further to the north and west. Therefore, the coast of Africa experiences clear weather during most of the year with extremely good vertical visibility.

The NE trade winds are responsible for the upwelling conditions off the NW African coast. During the summer months when the trades are located between 15°N and 35°N latitude, the principal component of the winds is northerly, therefore giving rise to the most intense upwelling conditions.

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[1] Colour illustrations have been printed with financial assistance from the Intergovernmental Oceanographic Commission.

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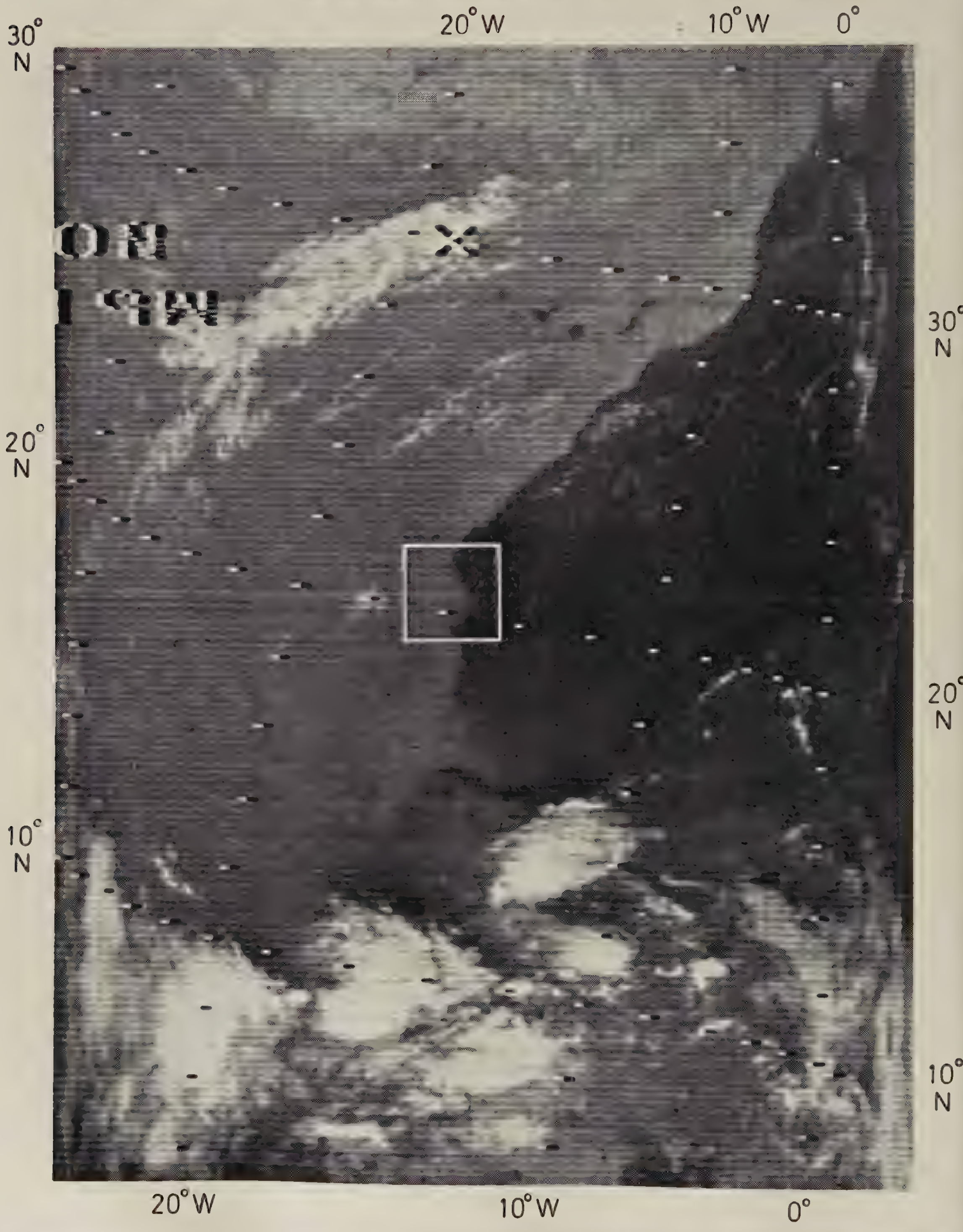
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Figure 1. Nimbus 5 thermal image of the NW coast of Africa taken 2 September 1973. Cap Blanc is located within the enclosure

Figure 1 shows a Nimbus 5 thermal image of the NW coast of Africa taken 2 September 1973, two days prior to the Skylab overpass. The clear conditions surrounding Cap Blanc indicate the influence of the offshore anticyclone and the low-moisture NE trade winds. The band of thick clouds to the south represents parts of the Intertropical Convergence Zone.

Spectral properties of plankton

Light penetration in water is affected by plankton, algae, and dissolved and suspended matter. As a result, the composition of backscattered light from the air-sea interface is determined by the nature of the constituents in the water column. In contrast to the absorption spectrum of chemically pure chlorophyll in solution, algae suspensions absorb and scatter light more uniformly throughout the visible part of the electromagnetic spectrum. Because of the spectral absorption and scattering properties of plankton, its concentration can be estimated by measuring the spectral backscattered radiance over water.

When monitoring plankton or biomass from high altitudes, we must consider the fact that algae behave more like a suspension than a pure solution of chlorophyll. As a result, solar light will be scattered at the outer shell of the plankton organisms. The absorption of incident irradiance by the cells depends on their outer structure and the optical density inside the cell. Variation in the optical density or the configuration of the cells may change the intensity of backscattered light even if the incident solar irradiance, sun angle, and chlorophyll concentration per unit of volume remain constant. Yentsch (1960) found that the red absorption band of chlorophyll has little influence on water colour. This means that the signal obtained with a red band sensor would record primarily the effect of backscattered light from the organisms.

Szekielda (1974) indicated that the size and concentration of particles or marine organisms seem to be the important contributors to the changes in backscattered light intensity as measured in the Skylab sensors. The scattering intensity of suspended particles is proportional to λ^{-n} where λ is the wavelength and n the Rayleigh value which may vary from 4 for pure water to 0 at high turbidity. In other words, the intensity of backscattered light increases with particle concentration. This shows the important influence of particles without chlorophyll on the backscattered light from below the sea surface. Lorenzen (1970) established a correlation between surface chlorophyll concentrations and primary productivity for different oceanic waters. Better correlations were found when chlorophyll and primary productivity data from the upwelling region off the NW coast of Africa were compared. This suggests that a significant relationship between the two parameters can be obtained when individual oceanic regions are studied, thus making surface chlorophyll measurements that much more valuable.

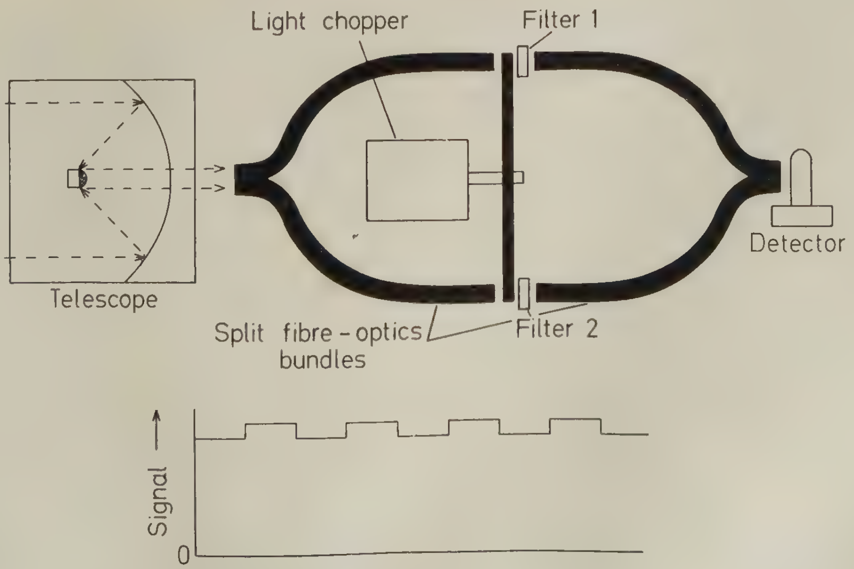


Figure 2. Differential radiometer for the detection of "chlorophyll" as developed by by Arvesen, Millard and Weaver (1973).

An often suggested algorithm of narrow band ocean colour reflectances was employed in an aircraft mission for evaluation of its effectiveness in chlorophyll determination and in recognition of changes in regional ocean colour distributions. A ratio of the 443 nm to the 525 nm reflectances has been discussed by Clarke and Ewing (1974) and Duntley (1972) as having the ability to determine chlorophyll concentration in near-surface waters from aircraft and satellite altitudes. From these observations Arvesen, Millard and Weaver (1973) developed a differential correlation radiometric method to detect chlorophyll. Their measurements of ratio values, using the continuous recording differential radiometer, correlated well with real-time sea-truth measurements of surface chlorophyll concentrations. From the results of flights over various types of water masses, a calibration of the reflectance ratio to surface chlorophyll concentrations (mg/m^3) was constructed.

During February and March 1974 the differential radiometric (DR) method, as shown in Figure 2, was used in an extensive oceanographic aircraft mission as part of the JOINT-I project in a one square degree region (20°–21° N latitude × 17°–18°W longitude) offshore of Cap Blanc. In comparison with surface chlorophyll sea-truth, the DR method was not effective in the determination of chlorophyll off Africa. Interferences caused by suspended particulates of eolian origin in the surface water plus presumed concentrations of Gelbstoff, resulted in an "enhanced" apparent chlorophyll signal. These interferences can be explained by the following: 1, increased backscattered radiance was caused by the high concentration of high refractive index (highly reflective) eolian and wave eroded particulates; 2, inherent optical properties including absorption by dissolved Gelbstoff, attenuation of radiance by sea water and particulate scattering (including multiple scattering) produced a spectral signal that the ratio method could not differentiate from that of chlorophyll; 3, selective scattering by phytoplankton and high non-selective scattering by the additional particulates in multiple events produced an increased backscattered signal to the DR which was an "enhanced" chlorophyll signature. These apparent chlorophyll signals were investigated in laboratory studies and were found to be principally attributed to the scattering properties of both inorganic particles and algae in suspension. The symmary of the study is shown in Figure 3.

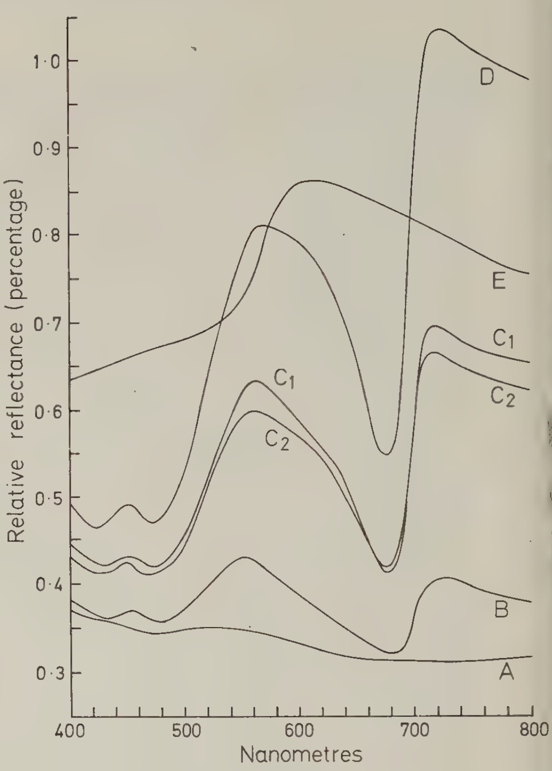


Figure 3. Reflection spectra of various samples: A, distilled water; B, dense algae sample, *Carteria* 4·86 × 10^4 mg/m^3 chl *a*; C_1, C_2, and D, mixed algae-clay suspensions; C_1 and C_2, sample B plus 1·0 ml of clay suspension 12·4 × 10^6 counts/ml; D, sample C plus 1·0 ml clay suspension; E, clay suspension 31 × 10^6 counts/ml.

Although this colour ratio did not effectively determine chlorophyll levels, there was a strong correlation between sea surface temperature (SST) gradients and the observed ocean colour ratio gradients. Higher ratios were coincident with low temperature, with only a few nearshore exceptions. A significant correlation between this colour ratio and total particulates from sea-truth measurements does exist and, in addition, increased fishing was observed to be closely associated with the SST-DR ratio gradients. Therefore, ocean colour changes associated with sea-surface temperature gradients are indicative of productive water masses off the NW coast of Africa.

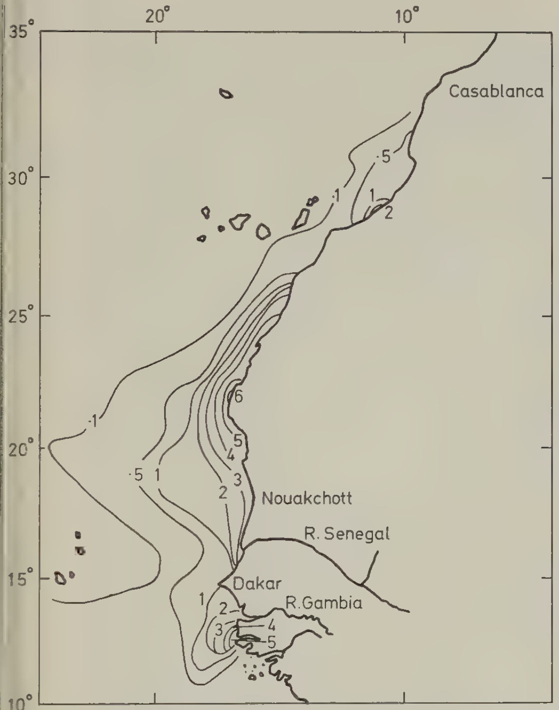
Cap Blanc

The upwelling in the vicinity of Cap Blanc is persistent throughout most of the year and is evident by the high concentrations of chlorophyll noted in Figures 4 and 5. A survey of fish tonnages between Cap Blanc and Cape Timiris was made by Boley (1974) in July 1973. High concentrations of fish were observed west of Cap Blanc while very high tonnages were noted near Cape Timiris. The tonnages of fish therefore, show some correlation with surface chlorophyll concentrations in this area.

During the 4. September 1973 overpass, Skylab collected radiometric data with the S190A Multispectral Camera, the S190B Earth Terrain Camera and the S192 Multispectral Scanner. The ground coverage provided by these sensors is shown in Figure 6. During the subsequent Skylab 4 mission, photographs were also taken of the study area with hand-held cameras.

Figure 7 is a high resolution colour photograph of the Banc d'Arguin taken with S190B Earth Terrain Camera. The scale of the photograph is approximately 1:900 000 in covering an area of 110 km × 110 km. There is an obvious colour gradient of blue to green from offshore to nearshore waters indicative of the presence of suspended material and Gelbstoff. Figure 8 is the green band S190A multispectral spectral image having a response region between 500 nm and 600 nm. The scale of this photograph is roughly 1:2·7 million covering an area of 157 km × 157 km. The patterns and patchiness of offshore suspended material are evident from this photograph.

The nearshore patterns of suspended material indicate a northerly flow of waters toward Cap Blanc. The plankton patch southwest of the Cap indicates a southerly drift of waters from north of the Cap. Using dynamic topography, Fedoseev (1970) discussed the geostrophic circulation of surface



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Casablanca
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·5
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Nouakchott
R. Senegal
Dakar
R.Gambia
1
2
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4
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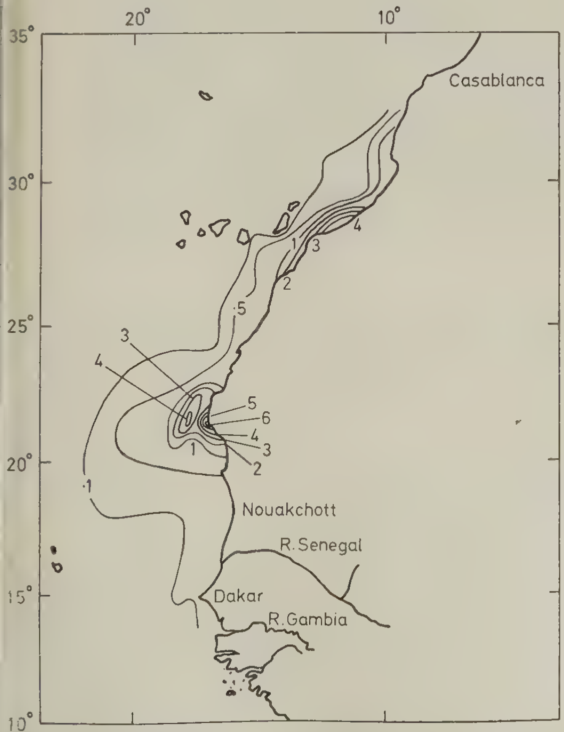
Figure 4. Composite of chlorophyll concentrations (mg/m^3) for the months January–June.



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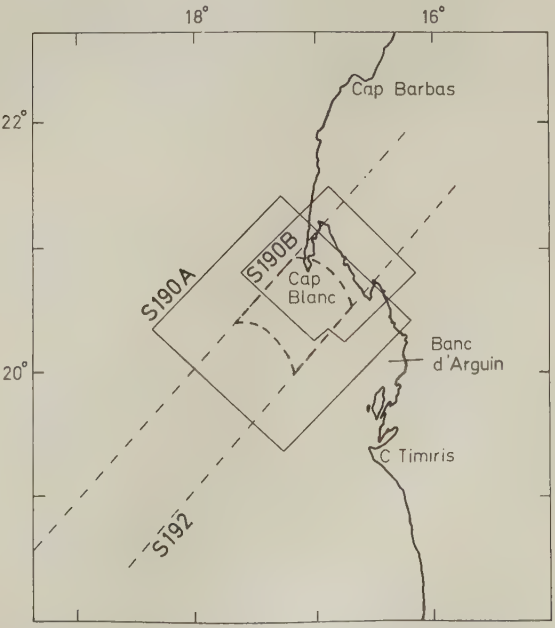
Nouakchott
R. Senegal
Dakar
R.Gambia

Figure 5. Composite of chlorophyll concentrations (mg/m^3) for the months July–September.



18°
16°
22°
20°
Cap Barbas
S190A
S190B
Cap Blanc
Banc d'Arguin
C Timiris
S192

Figure 6. Ground coverage provided by the Skylab sensors during the 4 September 1973 overpass.

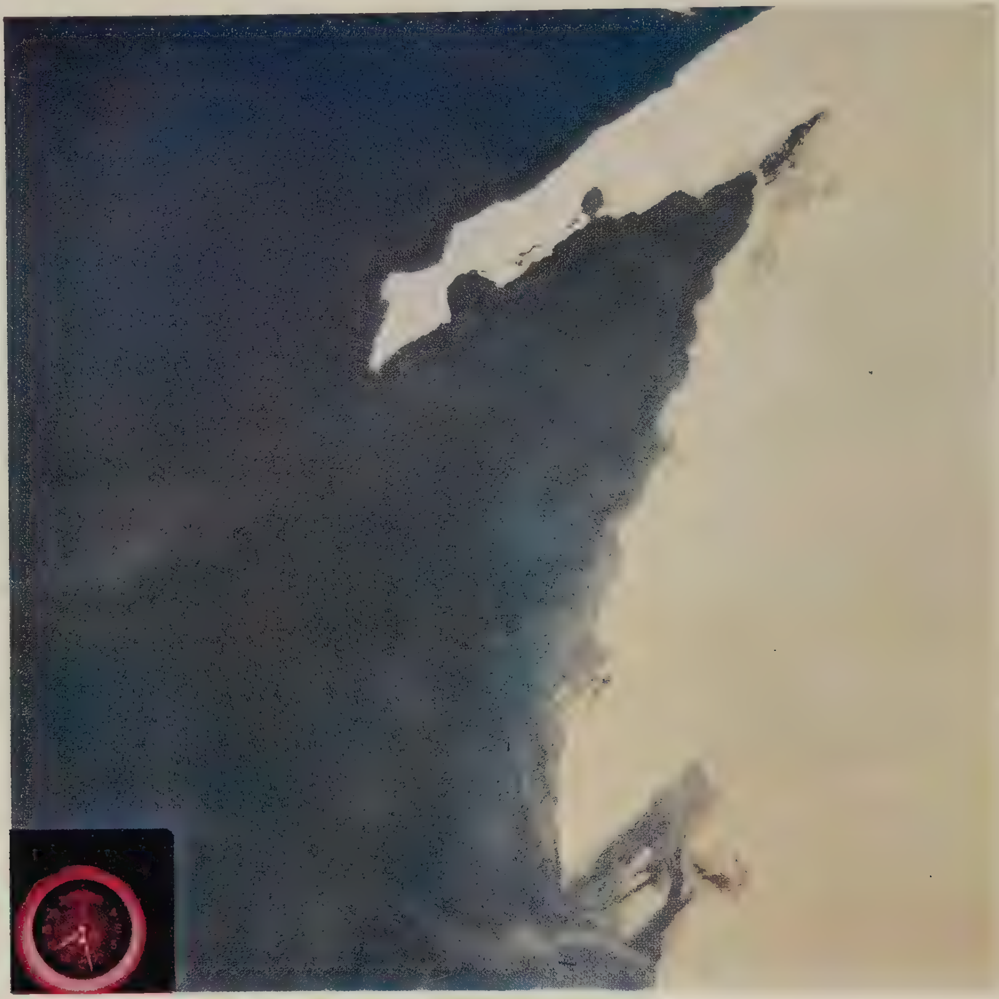


Figure 7. S190B colour photograph of Cap Blanc. For area covered see Figure 6.

waters in the shelf region and concluded that quasi-stationary gyres are formed in the eastern boundary of the Canary Current. The most stationary gyre south of Cap Blanc was observed throughout the year and the offshore patterns noted in the Skylab images are influenced by the flow of the gyre.

Szekielda (1974) reports that plankton patchiness varies especially with the change of seasons. A strong gradient of chlorophyll and/or plankton offshore of Cape Timiris is connected with the converging water masses from the Banc d'Arguin and has been detected in all four seasons. Figure 9 shows the location of offshore ocean colour boundaries as derived from ERTS-1 and Skylab. The southern gradients show seasonal positions between 1972 and 1973. Besides small-scale fluctuations, the gradient shifts over a maximum distance of only about 16 km. This is an indication that the offshore gradient is a fairly permanent feature. The enclosed lines south of Cap Blanc, are the relative positions of the suspended material patch observed from Skylab 3 and 4. Between September 1973 and January 1974, the patch experienced a broadening and shoreward movement. This may be a result of a seasonal change in the circulation.

Channel 13 of the multiscanner scanner of Skylab, recorded emitted thermal radiation from the surface of the earth. For the Cap Blanc overpass, the radiation data were converted to blackbody temperatures. A frequency distribution of the digitized radiation measurements (in relative units) within the test site was used to colour-code the different temperature intervals. Figure 10 shows the number of measurements (or counts) as a function of radiation units as

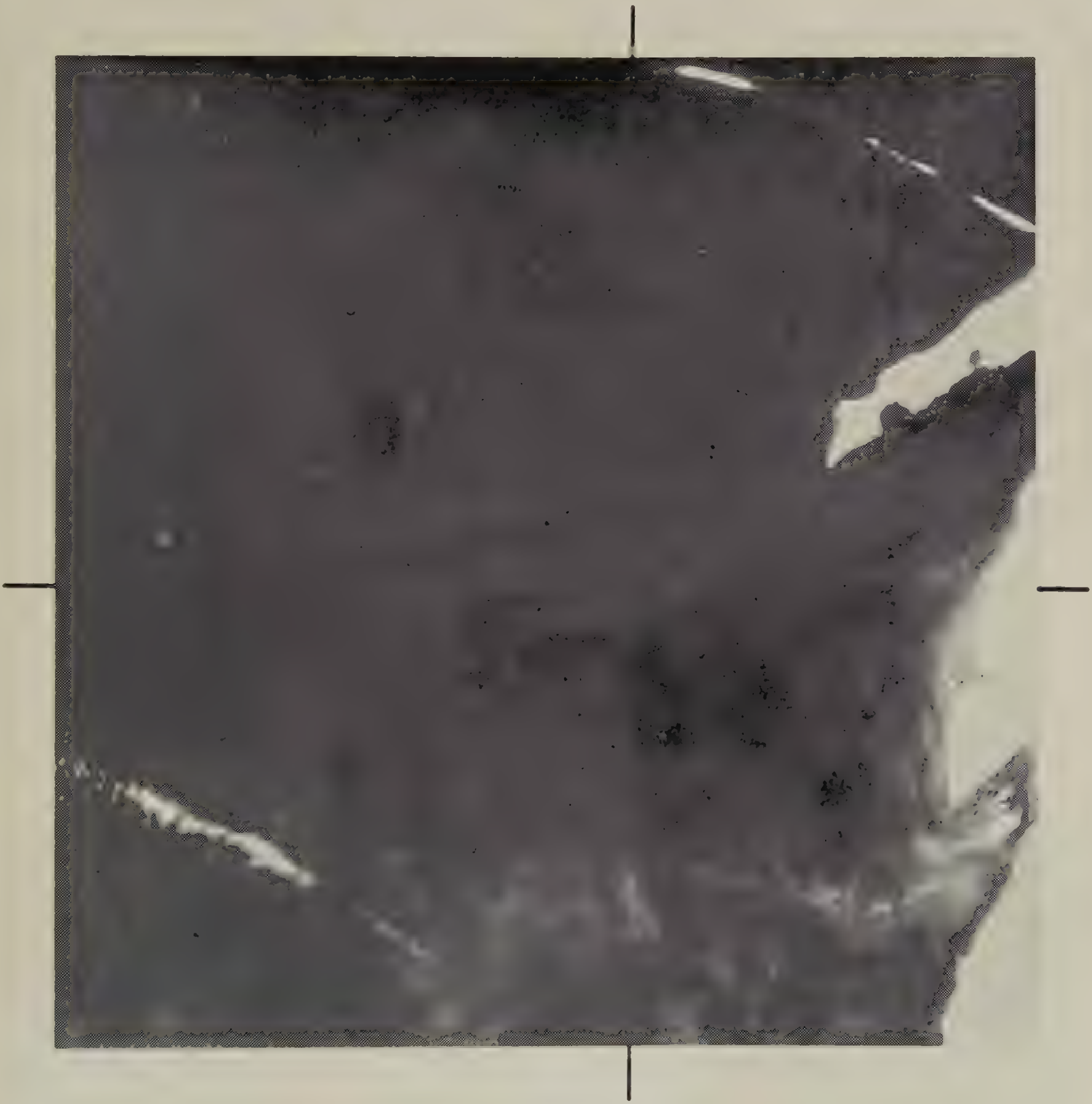


Figure 8. Green band S190A image of Cap Blanc. For area covered see Figure 6. The position of a U shaped patch of suspended material to the southwest of Cap Blanc is indicated by the intersection of the marker lines on the margin of the photograph.

well as the corresponding colour-code and temperatures. Figure 11 is a colour-coded temperature map of the waters off Cap Blanc. Although the temperatures have not been corrected for atmospheric effects, the relative temperature gradients can be used to locate the origin of upwelled waters. The cold patch of water in Figure 11 is shown to be roughly between 7°C and 11°C. Coldest known upwelling water off the African coast has only been reported to be as low as 14°C. Therefore it is estimated that the calculated blackbody temperatures are at least 4°C to 6°C colder than actually present. Since the cold patch directly corresponds to the suspended material pattern observed in the imagery, this is undoubtedly a source of upwelled water. In September 1972, Dr. Ballaster (Szekielda, 1974) observed a strong gradient of temperatures and fluorescence to the southwest of Cap Blanc.

As described previously, ocean colour changes associated with sea surface temperature gradients indicate productive water masses in this region. The Skylab spacecraft was effective in recording these

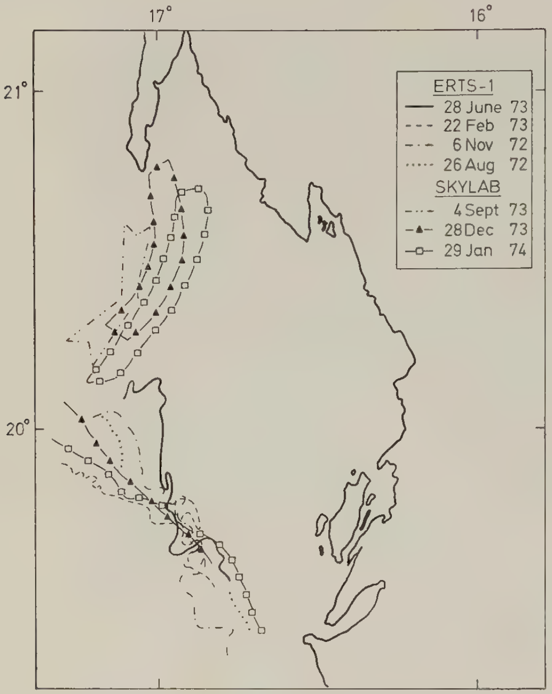

17°
16°
21°
20°
ERTS-1
28 June 73
22 Feb 73
6 Nov 72
26 Aug 72
SKYLAB
4 Sept 73
28 Dec 73
29 Jan 74

Figure 9. Offshore ocean colour boundaries derived from ERT S-1 and Skylab.

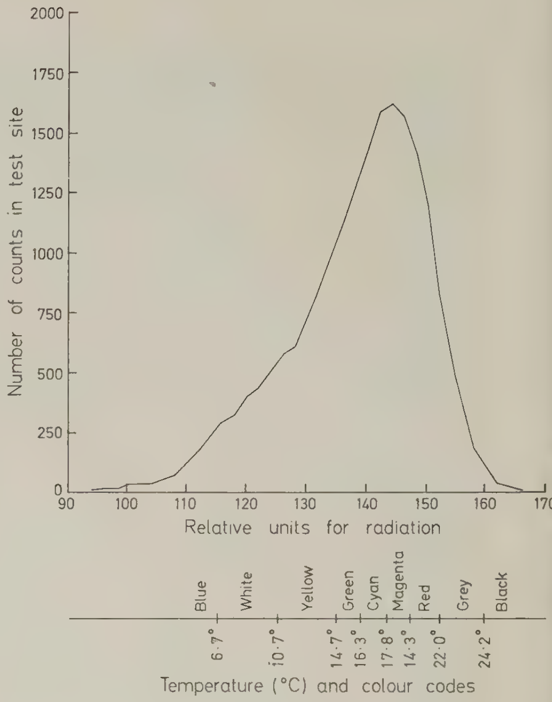


Figure 10. Thermal data and colour coding for S192 imagery.

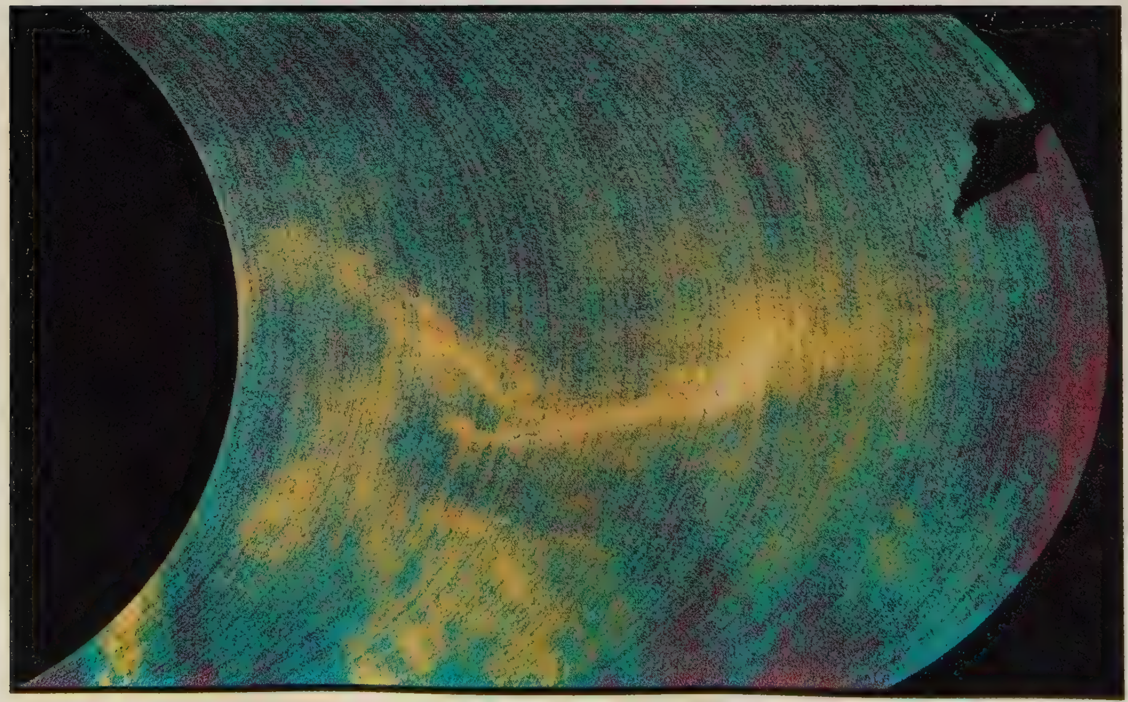


Figure 11. Colour-coded temperature distribution derived from channel 13 of the S192 multispectral scanner. For area covered see Figure 6.

gradients and it can therefore be determined that an intensive area of upwelling was present in September 1973. By correlating the observed ocean colour changes with the low temperature readings, an obvious area of productive waters was apparent offshore of Cap Blanc.

Conclusions

The spectral properties of the upwelled waters off the NW coast of Africa have been studied with observations derived from aircraft and Skylab. Results of the aircraft study indicate that the two-channel, ratio approach is ineffective in determining surface chlorophyll concentrations and should not be used in future studies. Ocean colour boundaries and temperature gradients were found to be directly correlated with each other in the upwelling region. Photographic and scanner data derived from Skylab has been effective in locating ocean colour boundaries and mapping temperature distributions. Both can be utilized in this region to qualitatively determine areas of high biological productivity. This simple correlation may be applicable in future efforts toward fishery resource management in upwelling areas.

Acknowledgements

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Etude du régime alimentaire de la Mourine vachette, *Pteromylaeus bovinus* (Geoffroy Saint-Hilaire, 1817) (Pisces, Myliobatidae) des côtes tunisiennes

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The study is based on the examination of 568 individuals (255 males, 313 females) caught in Tunisian waters in 1973–75. *Pteromylaeus bovinus* – the Bull ray – is a voracious species and the stomachs of over 70% of the individuals examined contained food. But the intake of adult females is reduced in summer when the eggs are shed. As with other bottom living elasmobranchs, benthic invertebrates and fish appear to be favoured as food. Teleosts form an important part of the diet in both young and older fish, and this somewhat exceptional feature is associated with the high growth rate of the Bull ray and an early change from demersal to a semi-pelagic life. *P. bovinus* will vary its diet by taking cephalopods and teleosts, and among the latter the pelagic species are the most important.

Introduction

La littérature ichthyologique ne fournit pratiquement aucun renseignement sur le régime alimentaire de *Pteromylaeus bovinus*. Dans l'ensemble, les auteurs, tout comme Dieuzeide, Novella et Roland (1953), mentionnent que cette espèce possède des "mœurs semblables à celles de *M. aquila*".

Dans un précédent travail concernant la biologie de *P. bovinus* nous avons donné quelques observations sur les aliments ingérés par ce sélacien: "*Pteromylaeus bovinus* se nourrit essentiellement d'invertébrés benthiques et occasionnellement de téléostéens. Les groupes zoologiques consommés sont par ordre de fréquence décroissante: gastéropodes; lamellibranches; crustacés décapodes; téléostéens (toujours difficiles à déterminer; nous avons pu néanmoins reconnaître des gobies et des blennies); échinodermes (astéries en majorité) et annélides polychètes (du genre *Hermione*)" (Capapé et Quignard, 1975).

Nous avons cru utile de faire un travail plus approfondi sur le régime alimentaire de *P. bovinus* afin de contribuer à une meilleure connaissance de l'espèce. L'analyse de l'alimentation de cet Hypotrême a été effectuée en fonction des saisons, du sexe et de l'âge.

Matériel et méthodes

Le matériel étudié a été capturé au chalut ou au trémail dans les eaux tunisiennes: dans le golfe de Tunis et surtout dans le golfe de Gabès, pendant les années 1973, 1974 et 1975.

L'analyse des contenus gastriques a été effectuée sur du matériel frais, le plus souvent en bon état de conservation. Nous avons disséqué au total 568 individus (255 mâles et 313 femelles).

Pour l'étude des contenus stomacaux, nous donnons:

1. le coefficient de réplétion (CR) défini comme le pourcentage d'estomacs pleins ou contenant des restes de nourriture par rapport au nombre total d'estomacs examinés (Quignard, 1966; Du Buit, 1968).
2. l'indice de fréquence (IF) des proies qui est le rapport du nombre d'estomacs contenant un certain groupe zoologique de proies au nombre total d'estomacs pleins.

Coefficient de réplétion et indice de fréquence sont donnés pour les quatre saisons: printemps (P), été (E), automne (A), hiver (H).

Les mâles et les femelles sont étudiés séparément et pour chaque sexe jeunes et adultes. Sont considérés comme adultes tous les individus ayant atteint ou dépassé la taille de première maturité sexuelle.

Le long des côtes tunisiennes, les mâles sont adultes à partir de 80 cm d'envergure discale; les premières femelles adultes observées mesuraient 90 cm de large et il semble qu'après 100 cm toutes le soient (Capapé et Quignard, 1975).

Présentation des resultats

Coefficient de réplétion (Tableau 1, Figure 1)

Le coefficient de réplétion des jeunes individus mâles et femelles présentent peu de fluctuations saisonnières augmentant faiblement en été et en automne.

Le coefficient de réplétion des mâles adultes est pratiquement uniforme, se maintenant à des valeurs élevées durant toute l'année; celui des femelles adultes est moins stable, il accuse un net fléchissement en été, il remonte à l'automne pour atteindre un maximum en hiver.

Analyse qualitative et quantitative des groupes zoologiques ingérés (Tableau 2, Figure 2)

Les mâles et les femelles juvéniles consomment presque toujours des lamellibranches (IF = 1) et en moindres quantités d'autres invertébrés benthiques comme les gastéropodes, les céphalopodes, les crustacés, les annélides polychètes, les échinodermes et les sipunculiens. Les estomacs des jeunes individus de chaque sexe contiennent fréquemment des téléostéens qui constituent après les lamellibranches, les proies les plus abondamment ingérées.

Les mâles et les femelles adultes absorbent les mêmes organismes zoobenthiques que les exemplaires juvéniles mais les indices de fréquence sont moins élevés et de plus, la part des téléostéens dans leur régime alimentaire devient prépondérante.

Il faut remarquer que pour chaque catégorie d'individus examinés les fluctuations saisonnières sont peu marquées au niveau des groupes zoologiques préférentiels.

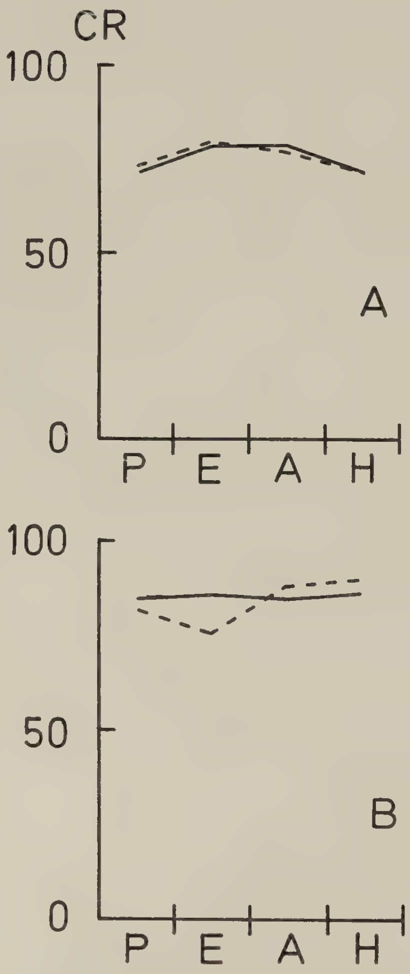

Figure 1. Mise en évidence du coefficient de réplétion en fonction du sexe, de l'âge et des saisons: printemps (P), été (E), automne (A), hiver (H).
A: individus juvéniles ——— mâles
B: individus adultes – – – – femelles

Notons enfin que pour l'ensemble des individus (Tableau 2 C), les lamellibranches (IF = 0·75), les téléostéens (IF = 0·64), les céphalopodes (IF = 0·41), les gastéropodes (IF = 0·34) et les crustacés (IF =

Tableau 1. Variation du coefficient de réplétion en fonction du sexe de l'âge et des saisons pour *Pteromylaeus bovinus*

Sexe	Mâles (255)								Femelles (213)							
Age	Jeunes (129)				Adultes (126)				Jeunes (169)				Adultes (144)			
Saisons	P	E	A	H	P	E	A	H	P	E	A	H	P	E	A	H
Nombre individus.......	28	36	31	34	32	29	34	31	41	48	46	34	29	40	35	40
Estomacs pleins........	20	28	23	24	27	25	28	25	30	38	36	24	24	26	31	36
Coefficient de réplétion..	71	78	78	71	85	86	85	86	73	79	77	71	82	76	88	90

Tableau 2. Analyse qualitative et quantitative des groupes zoologiques ingérés en fonction du sexe, l'âge et des saisons pour *Pteromylaeus bovinus*. Nombre d'estomacs pleins et les indices de fréquence (IF)

A. Cas des mâles

	Jeunes				Adultes			
Saisons	P	E	A	H	P	E	A	H
Groupes zoologiques								
Lamellibranches	20	28	23	24	12	10	13	11
	(1)	(1)	(1)	(1)	(0·44)	(0·40)	(0·46)	(0·44)
Gastéropodes.............	10	13	12	12	4	5	6	5
	(0·50)	(0·46)	(0·52)	(0·50)	(0·15)	(0·20)	(0·21)	(0·20)
Céphalopodes.............	7	11	11	10	14	14	15	13
	(0·35)	(0·39)	(0·48)	(0·42)	(0·52)	(0·56)	(0·53)	(0·52)
Crustacés.................	4	6	5	6	4	5	8	4
	(0·20)	(0·21)	(0·24)	(0·24)	(0·15)	(0·20)	(0·28)	(0·16)
Téléostéens...............	10	12	12	12	21	17	22	15
	(0·50)	(0·43)	(0·52)	(0·50)	(0·77)	(0·68)	(0·78)	(0·60)
Annélides	1	2	4	2	2	1	2	2
	(0·05)	(0·07)	(0·16)	(0·10)	(0·08)	(0·04)	(0·07)	(0·08)
Autres groupes............	2	2	4	3	4	1	2	4
	(0·10)	(0·07)	(0·16)	(0·12)	(0·16)	(0·04)	(0·07)	(0·16)

B. Cas de femelles

	Jeunes				Adultes			
Saisons	P	E	A	H	P	E	A	H
Groupes zoologiques								
Lamellibranches	30	38	36	24	11	16	14	16
	(1)	(1)	(1)	(1)	(0·46)	(0·44)	(0·45)	(0·44)
Gastéropodes.............	13	16	18	13	6	5	6	7
	(0·44)	(0·42)	(0·50)	(0·54)	(0·25)	(0·14)	(0·19)	(0·19)
Céphalopodes.............	9	11	11	10	11	12	11	16
	(0·39)	(0·28)	(0·30)	(0·42)	(0·46)	(0·33)	(0·35)	(0·44)
Crustacés.................	6	8	5	6	4	7	5	6
	(0·20)	(0·20)	(0·15)	(0·25)	(0·16)	(0·19)	(0·16)	(0·16)
Téléostéens...............	15	17	18	12	20	30	24	30
	(0·50)	(0·48)	(0·50)	(0·50)	(0·83)	(0·83)	(0·77)	(0·83)
Annélides	2	2	2	2	2	2	4	3
	(0·06)	(0·05)	(0·06)	(0·08)	(0·08)	(0·05)	(0·12)	(0·08)
Autres groupes............	2	0	0	1	2	3	2	3
	(0·6)			(0·04)	(0·08)	(0·08)	(0·06)	(0·08)

C. Ensemble des individus

Groupes zoologiques	Nombre total	I F
Lamellibranches	336	0·74
Gastéropodes	151	0·34
Céphalopodes	186	0·41
Crustacés	89	0·20
Téléostéens	287	0·64
Annélides	35	0·08
Autres groupes	39	0·08

0·20) constituent la base fondamentale du régime alimentaire de *Pteromylaeus bovinus* des côtes tunisiennes. Les annélides polychètes (IF = 0·08) et les individus d'autres groupes comme les sipunculiens, les échinodermes et les sélaciens ne sont consommés qu'occasionnellement voire accidentellement.

Analyse spécifique des proies ingérées (Tableau 3)

Il apparait dans le Tableau 3 que les espèces-proies les plus souvent trouvées dans les estomacs examinés appartiennent toutes ou presque aux groupes zoologiques précédemment cités.

Néanmoins, nous avons rencontré quelques difficultés dans l'identification des lamellibranches et des gastéropodes, *Pteromylaeus bovinus* comme *Myliobatis aquila* "broie les coquilles pour en extraire l'animal et en rejette les débris". (Capapé, 1975).

Parmi les lamellibranches dont nous avons pu faire la diagnose, nous avons reconnu quelques espèces du genre *Chlamys* (77), *Pecten jacobaeus* (24), *Tellina incarnata* (24) et *Venus gallina* (23).

Chez les gastéropodes figurent les nudibranches en général (20), *Thetys leporina* (18), *Pleurobranchea meckeli* (17) en particulier.

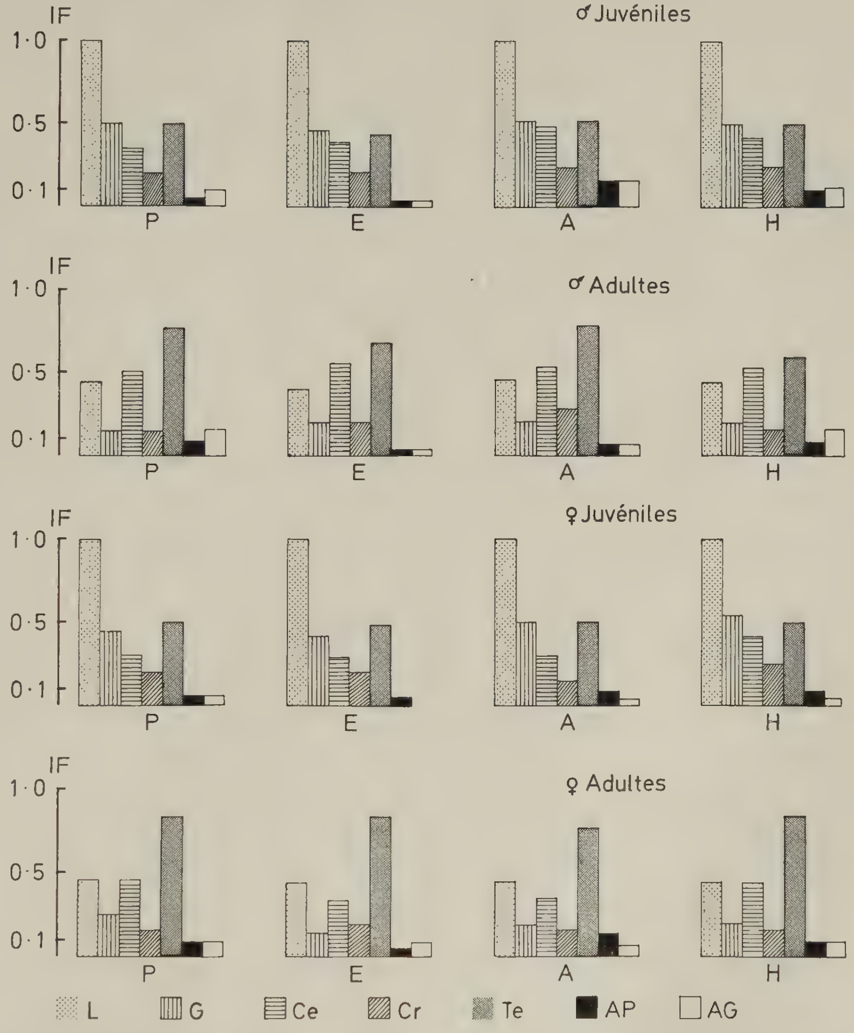

Figure 2. Indice de fréquence des principaux groupes zoologiques en fonction du sexe, de l'âge et des saisons: printemps (P), été (E), automne (A), hiver (H). L, Lamellibranches; G, Gastéropodes; Ce, Céphalopodes; Cr, Crustacés; Te, Téléostéens; AP, Annélides polychètes; AG, autres groupes.

Il n'existe véritablement pas d'espèces préférentielles chez les crustacés consommés par *P. bovinus*; notons la relative abondance dans les contenus gastriques de *Squilla mantis* (13), et d'*Alpheus ruber* (15).

Parmi les céphalopodes ce sont pratiquement les mêmes espèces qui sont déterminées dans l'appareil digestif de la mourine vachette: *Sepia officinalis* (39), *Sepia elegans* (34), *Loligo vulgaris* (31). Il faut toutefois préciser que *Sepiola rondeleti* (28) est capturé par les jeunes individus, *Eledone moschata* (28) et *Octopus vulgaris* (19) par les adultes.

Un nombre important d'espèces (23 au moins) de téléostéens a été identifié dans les estomacs disséqués. Il en résulte que parmi ces téléostéens peu ont été souvent rencontrés. Notons surtout la présence fréquente de pleuronectiformes, de *Blennidae*, de *Gobiidae* et de *Merlucius merlucius* (21) chez les individus juvéniles; les adultes capturant essentiellement des poissons pélagiques comme *Argentina sphyraena* (26) et *Sardina pilchardus* (20).

Analyse de la voracité (Fig. 3)

Contrairement aux autres sélaciens dont nous avons précédemment étudié le régime alimentaire, nous avons très fréquemment trouvé dans les contenus gastriques de *P. bovinus* plusieurs espèces différentes

Tableau 3. Liste et quantitées des genres ou espèces identifiées dans les contenus stomacaux de *Pteromylaeus bovinus* en fonction du sexe, de l'âge et des saisons

Sexe	Mâles								Femelles								
Ages	Jeunes				Adultes				Jeunes				Adultes				
Saisons	P	E	A	H	P	E	A	H	P	E	A	H	P	E	A	H	Total
Nombre d'estomacs	28	36	31	34	32	29	34	31	41	48	46	34	29	40	35	40	568
Annélides polychètes																	
Nereis sp.	–	1	1	–	–	–	–	1	–	–	–	1	1	1	1	1	8
Platynereis dumerilii	–	–	–	–	1	1	–	–	–	1	–	–	–	–	–	–	3
Hermione hystrix	1	1	2	1	1	–	–	–	1	1	1	–	–	1	2	1	13
Aphrodites aculeata	–	–	1	–	–	–	1	–	–	–	–	1	–	–	–	–	3
Indéterminables	–	–	1	1	–	–	1	1	1	–	1	–	1	1	1	1	10
Sipunculiens																	
Sipunculus nudus	2	–	–	1	1	–	–	–	–	–	–	–	–	1	–	–	5
Indéterminables	–	–	–	1	–	–	–	–	–	–	–	–	–	–	–	–	1
Gastéropodes																	
Calliostoma zizyphinus	2	–	–	1	–	1	1	–	1	1	1	1	–	1	–	1	11
Natica catena	2	1	–	–	–	–	1	–	1	–	2	–	1	–	1	1	10
Natica millepunctata	2	2	–	1	–	–	–	–	–	–	1	1	–	–	–	–	7
Natica sp.	–	2	–	1	–	1	–	–	1	2	2	–	–	–	–	–	9
Murex	–	–	2	1	–	–	–	–	–	–	1	1	–	–	–	–	5
Tritonalia erinacea	–	1	2	2	1	–	–	–	–	1	1	–	–	–	–	1	9
Bullaria striata	–	2	–	2	–	–	1	–	1	1	2	2	–	1	1	–	13
Tethys leporina	–	–	2	2	–	2	3	–	3	3	1	2	–	–	–	–	18
Pleurobranchea meckeli	2	1	3	1	–	–	–	2	2	2	2	–	1	–	1	–	17
Nudibranches	1	1	1	–	1	–	–	1	2	3	1	4	2	1	1	1	20
Indéterminables	1	3	2	1	2	1	1	2	2	3	2	2	3	2	2	2	31
Lamellibranches																	
Chlamys opercularis	2	4	2	1	1	1	1	–	2	3	4	1	1	–	1	1	25
Chlamys glabra	2	4	2	1	1	1	1	–	2	3	3	1	1	–	1	1	24
Chlamys varius	2	2	2	4	1	–	1	1	1	1	3	2	2	2	1	3	28
Pecten jacobaeus	2	2	1	1	–	1	–	1	4	3	3	3	–	1	1	1	24
Cardium aculeatum	–	1	–	1	–	–	–	–	1	1	2	1	–	–	–	–	7
Cardium edule	1	3	–	–	–	–	–	1	3	1	1	1	–	–	–	–	11
Venus gallina	2	3	3	2	2	1	1	–	1	1	2	2	–	2	1	–	23
Venus verrucosa	1	1	1	1	–	–	–	1	1	1	1	–	–	2	1	–	11
Venus casina	1	1	2	2	2	1	1	1	2	1	1	1	1	1	1	–	19
Tellina incarnata	1	2	3	1	1	–	1	–	3	4	3	1	1	1	1	1	24
Mactra corallina	–	1	2	1	2	–	1	1	2	3	1	1	–	–	1	1	17
Solen marginatus	4	2	–	1	–	1	1	1	1	1	2	1	1	1	–	–	17
Indéterminables	4	3	5	8	2	4	5	4	7	16	10	10	4	8	6	8	104
Céphalopodes																	
Sepia officinalis	1	1	3	1	4	3	2	2	1	1	3	1	5	3	3	5	39
Sepia elegans	1	3	1	1	2	3	3	2	3	2	3	3	2	1	3	1	34
Sepiola rondeleti	1	2	2	3	1	2	2	2	3	2	1	3	–	3	–	1	28
Loligo vulgaris	2	1	2	3	2	2	3	1	2	2	2	2	2	2	2	1	31
Alloteuthis media	–	1	–	1	1	1	–	1	–	1	–	–	–	–	–	2	8
Eledone moschata	2	1	3	1	1	1	3	2	–	3	2	1	1	2	2	3	28
Octopus vulgaris	1	2	–	–	4	2	2	1	–	–	–	–	1	1	1	4	19
Crustacés																	
Squilla mantis	–	1	–	1	–	1	1	1	1	2	–	1	1	1	1	1	13
Peneus kerathurus	–	1	–	–	–	–	–	–	–	–	–	1	–	–	1	1	4
Alpheus ruber	1	2	–	1	1	–	1	1	1	2	1	1	1	1	–	1	15
Sycionia carinata	1	2	1	1	1	–	–	–	1	–	–	1	–	–	–	–	8
Aegeon cataphractus	–	–	1	–	–	–	–	–	–	–	1	–	–	–	–	–	2
Eupagurus sp.	2	2	–	–	–	–	2	2	1	2	1	–	1	2	1	1	17
Dardanus arrosor	–	–	–	–	–	1	2	1	–	1	–	–	–	1	1	1	8
Dorippe lanata	–	–	1	–	–	2	–	–	–	1	–	–	–	–	–	–	4
Atelecyclus rotundatus	–	–	1	–	2	–	–	–	1	–	–	–	–	1	–	1	6
Macropipus puber	–	–	–	1	1	2	–	–	–	–	–	–	–	–	–	–	4
Goneplax rhomboides	–	1	–	–	1	2	–	–	–	–	–	1	1	–	1	1	8
Inachus dorsettensis	–	–	–	–	–	–	–	–	–	–	1	–	–	1	–	2	4

(suite p. 219)

Tableau 3. (suite)

Sexe	Mâles								Femelles								
Ages	Jeunes				Adultes				Jeunes				Adultes				
Saisons	P	E	A	H	P	E	A	H	P	E	A	H	P	E	A	H	Total
Nombre d'estomacs	28	36	31	34	32	29	34	31	41	48	46	34	29	40	35	40	568
Pilimnus hirtellus	–	–	–	1	–	–	1	–	–	–	2	–	–	–	–	–	4
Indéterminables	–	1	1	2	–	–	2	–	2	1	1	1	1	–	1	1	14
Echonidermes																	
Echinaster sepositus	1	–	1	1	1	1	1	1	1	–	–	1	1	1	–	2	13
Astropecten spinulosus	–	1	2	2	1	–	–	–	–	–	–	–	–	–	1	–	7
Astropecten aurantiacus	–	–	–	–	–	–	1	1	–	–	–	–	1	–	–	1	4
Ophioderma longicauda	–	–	1	–	–	–	–	–	1	–	–	–	–	–	–	–	2
Sélaciens																	
Raja miraletus	–	1	–	–	1	–	–	–	–	–	–	–	–	1	1	1	5
Raja radula	–	–	–	–	–	–	–	2	–	–	–	–	–	–	–	–	2
Téléostéens																	
Sardina pilchardus	–	1	–	–	2	1	3	1	–	–	–	–	1	3	3	5	20
Sardinella aurita	–	1	–	–	1	1	1	1	1	2	1	–	1	2	2	1	15
Alosa finta	–	–	–	–	1	1	–	2	–	2	1	–	2	2	1	1	13
Engraulis encrasicholus	–	–	–	–	3	1	2	2	1	1	–	–	2	1	2	1	16
Argentina sphyraena	2	1	2	1	3	1	1	1	–	2	2	–	1	4	2	3	26
Conger conger	1	–	1	1	1	–	–	1	–	–	–	–	1	–	–	1	7
Merlucius merlucius	1	1	2	2	3	2	–	–	2	2	1	1	–	2	1	1	21
Paracentropristis hepatus	–	1	1	–	–	–	1	–	1	1	1	–	–	3	1	1	11
Cepola rubescens	–	–	–	1	–	1	1	1	–	–	–	–	1	–	–	2	7
Mullus sp.	–	1	–	2	–	2	1	–	–	1	2	–	–	3	2	2	16
Maena maena	–	–	–	1	1	1	–	–	1	1	2	–	–	3	2	3	15
Pagellus erythrinus	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–	1	3
Boops boops	–	1	–	–	–	–	–	–	–	–	–	–	–	–	–	1	2
Callionymus lyra	–	–	–	–	–	–	2	–	–	1	1	–	–	1	1	–	6
Blennius ocellaris	1	–	–	1	2	1	1	1	2	–	3	1	1	2	2	2	20
Blennius sp.	1	–	–	1	2	2	2	–	2	–	1	1	–	2	1	3	18
Gobius quadrimaculatus	–	1	–	1	–	2	2	–	1	1	1	2	–	1	1	–	13
Gobius jozo	1	1	–	–	1	1	2	–	1	1	2	2	–	1	2	–	15
Gobius sp.	2	–	–	1	1	1	1	–	1	1	2	2	–	1	2	1	16
Lepadogaster gouani	–	–	–	–	–	–	1	–	–	–	–	–	–	–	–	–	1
Solea solea	1	2	–	–	–	1	2	1	–	1	1	1	1	1	1	2	15
Microchirus ocellatus	–	–	–	–	–	–	1	1	–	1	1	1	1	1	1	1	9
Citharus macrolepidotus	–	–	–	–	–	–	–	2	–	1	–	1	2	1	–	–	7
Indéterminables	1	–	–	–	–	1	2	2	1	–	1	1	2	–	1	2	14

appartenant à divers groupes zoologiques. La Figure 3 montre que le plus souvent nous avons déterminé de 3 à 8 espèces différentes dans un même estomac, le maximum observé atteignant 14 chez deux exemplaires.

Discussion

L'étude du régime alimentaire de *Pteromylaeus bovinus* montre que ce sélacien est une espèce extrêmement vorace. Cette voracité est très marquée aussi bien sur le plan quantitatif avec un coefficient de réplétion élevé toute l'année (quels que soient le sexe et l'âge des individus) que sur le plan qualitatif avec un nombre toujours important d'animaux déterminés dans les estomacs examinés.

La voracité de *P. bovinus* n'explique pas à elle seule la faiblesse relative des variations saisonnières du coefficient de réplétion enregistré pour l'ensemble des exemplaires. Il faut également tenir compte d'autres facteurs comme probablement l'extrême habileté des spécimens dans la recherche et la capture des proies mais aussi et surtout de la richesse du golfe de Gabès en invertébrés benthiques et en téléostéens comme certains *Clupeidae* notamment (Ktari-Chakroun et Azouz, 1971; Ben Othman, 1971).

Chez les femelles adultes, par contre, la baisse du coefficient de réplétion en été semble directement liée à la reproduction de l'espèce. En effet, Capapé et Quignard (1975) ont observé en quantités relativement importantes des femelles parturiantes ou sur le point de mettre bas. Il se pourrait donc que la par-

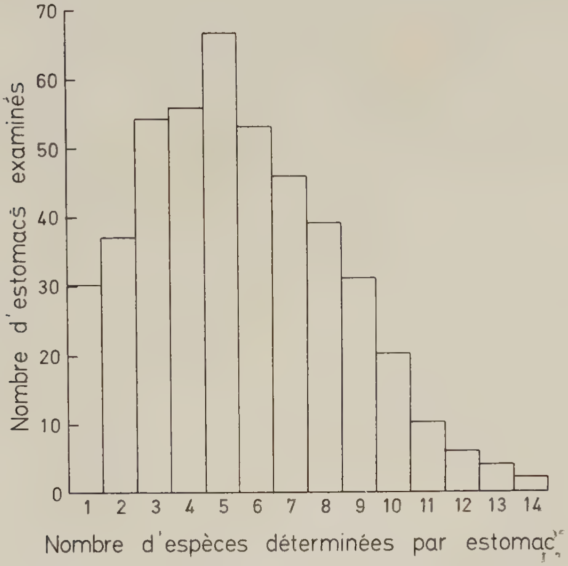

Figure 3. Mise en évidence du nombre d'espèces ingérées dans un certain nombre d'estomacs examinés.

turition détourne les spécimens adultes de la recherche de la nourriture.

L'examen des contenus stomacaux de l'ensemble des individus fait apparaître que le régime alimentaire de *P. bovinus* se rapproche de celui de *Myliobatis aquila* précédemment étudié (Capapé, 1975). En effet les deux espèces utilisent pour se nourrir les invertébrés benthiques en général et les téléostéens. Néanmoins, si les jeunes de *P. bovinus* consomment en abondance les invertébrés benthiques, ils capturent davantage de téléostéens que les jeunes de *M. aquila*. Ce phénomène est dû au fait que les exemplaires de la mourine vachette ont dès la naissance une taille plus grande que celle de l'aigle de mer. Ils sont donc plus rapidement aptes à chasser certaines proies comme les téléostéens. Notons également que pour les mêmes raisons nous avons plus souvent identifié des céphalopodes dans les estomacs des jeunes de *P. bovinus*.

De ce fait, s'il existe un changement spécifique des proies préférentielles chez ce Myliobatidae, il est toutefois moins marqué que pour les autres sélaciens quelle que soit l'espèce ou la zone marine comme par exemple les Rajidae des côtes britanniques (Holden et Tucker, 1974) francaises (Du Buit, 1968) ou tunisiennes (Capapé et Azouz, 1975).

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The dispersal of plaice eggs and larvae in the Southern Bight of the North Sea

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Investigations of the dispersal of the eggs and larvae of the plaice in the Southern Bight of the North Sea have involved measurement of the egg and larval distributions, the dye tracer Rhodamine-B and an array of moored current meters. The spread of the egg and larval distributions changed little as the eggs and larvae developed, suggesting that turbulent diffusion was at a comparatively slow rate. This conclusion was supported by the results of the tracer experiment and the application of a mathematical model of diffusion. In this area the vertical shear diffusion process is much more important than horizontal turbulence in producing dispersal. The current meter results showed that in the central Southern Bight there was little difference between water movements at different geographical positions. Provided that attention was confined to water movements along the main tidal axis, the current meter results and the movement of the Rhodamine patch showed a constant proportionality to water movements through the Dover Strait. A marked difference between the northeasterly drift of larvae in 1962 and 1969 was found to correspond to similar differences in the flow through the Dover Strait.

Introduction

In the early part of 1969 a programme of investigations was carried out in the Southern Bight of the North Sea. The work dealt with hydrographic features relevant to the transport and dispersal of eggs and larvae of the plaice, for which the area is a major spawning ground. The investigations began in late January, which is usually the peak of the plaice spawning season, and continued until early April, thus covering a large part of the larval development period. Five surveys of the egg and larval distributions were made and the results are interpreted below in terms of the likely dispersal rates. These results are also compared with a similar set of data obtained in the same area in 1962.

The 1969 programme included the measurement of hydrographic parameters; water movements were measured using an array of moored recording current meters and diffusion rates using the Rhodamine-B technique. A description of the egg and larval investigations is given below and this is followed by an account of the hydrographic work.

Investigation of the distribution of plaice eggs and larvae

The 1969 survey of the distribution of plaice eggs and larvae in the Southern Bight of the North Sea was one of a series of similar investigations carried out in the North and Irish Seas in recent years. These surveys have concentrated particularly on the Southern Bight of the North Sea where well-defined distributions of eggs and larvae have been detected. Their primary purpose was to further a study of the biology of various species of fish and especially that of the plaice. One striking feature illustrated by the results is the high degree of mortality during the pelagic development stage, which, from laying of the eggs to larval metamorphosis, is of the order of 99·9% (Harding and Talbot, 1973). The main factor contributing to mortality is probably predation but there could also be a significant contribution from diffusion. A secondary consideration in the analysis of the results of all the surveys has thus been the determination of the diffusion rates and the 1969 investigations were planned with this factor particularly in mind. One of the well recognised features of the diffusion process is its dependence on scale, that is to say, on the size of the diffusing system. In fact the egg and larval distributions have dimensions of the order 50–200 km, a range for which very little observational data are available, as is illustrated by Okubo's (1971) summary of diffusion results (Fig. 1). One of the small number of experiments carried out on a fairly large diffusing system was the ICES experiment RHENO (Weidemann, 1973) but this took place in the northern North Sea where conditions governing diffusion differ from those in the Southern

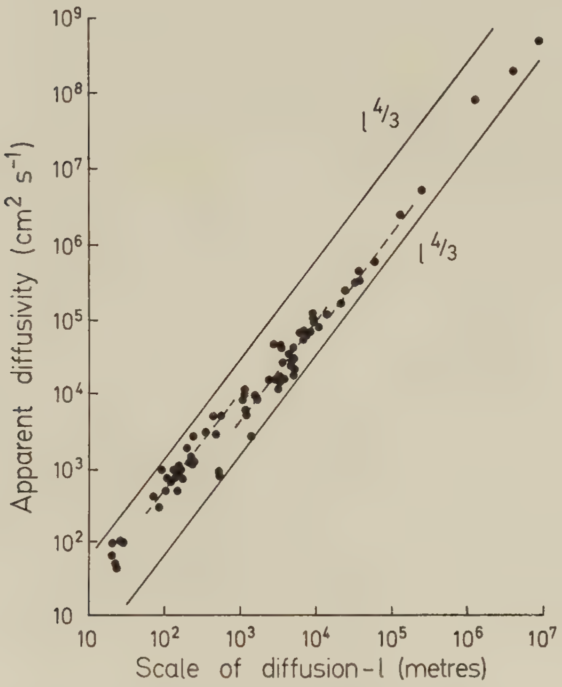


Figure 1. Okubo's summary of diffusion results showing, for comparison, lines representing a dependence of the diffusion coefficient on the 4/3 power of the scale of diffusion.

Bight and even this experiment dealt with a distribution whose linear dimensions reached only about 30 km.

An attempt to deduce diffusion rates from populations having a high mortality must involve a number of simplifying assumptions: in this case it has been assumed that mortality of eggs and larvae is not density-dependent and also that the distribution of newly-spawned eggs does not change appreciably over the period of a few days needed for a survey. The basic data and the method of analysis used will first be described. The results obtained in 1969 will then be discussed and some comparison made with results for other years.

The basic data

Data has been used from surveys in 1962, 1963 and 1969 and the times of these are given in Table 1. Each survey of an egg or larval distribution consists of over a hundred stations at each of which a plankton sample is taken using a modified Gulf III high-speed tow net (Bridger, 1958) which sweeps the water column from the surface to 2 m above the bottom and back, the water temperature being measured at the surface. For each plankton sample the number of plaice eggs or larvae at each of 10 development stages is counted according to a scheme based, for eggs, on the classifications of Apstein (1909), as given in Table 2a. The larval development stages

Table 1. Dates and times of surveys of plaice egg and larval distributions

Survey	Duration		
	1962	1963	1969
1	23–31 Jan	24–26 Jan	25–27 Jan
2	6–10 Feb	4–11 Feb	4– 6 Feb
3	15–20 Feb	15–19 Feb	12–14 Feb
4	25 Feb– 1 Mar		21–25 Feb
5	5–10 Mar		31 Mar– 6 Apr
6	14–20 Mar		
7	25 Mar– 1 Apr		

Table 2. Classification of egg and larval development stages

(a) Eggs

Apstein's classification	Equivalent stage used in this work
1– 4	1a
5– 6	1b
7–11	2
12–16	3
17–21	4
22–24	5

(b) Larvae

Ryland's classification	Equivalent stage used in this work
1a–d	6
2a, b	7
3a–c	8
4a, b	9

Table 3. Parameters used in Equation (1) for various development stages

	Stage	a	b
Egg	1a	6·1309	−5·0057
	1b	11·7269	−9·6197
	2	21·5293	−17·8264
	3	31·0769	−25·1373
	4	40·3652	−32·1041
	5	53·7056	−42·0072
Larva	6	50·2695	−40·6187
	7	125·9762	−105·0667
	8	207·3563	−170·8958
	9	299·6352	−244·66

recognized were the first four described by Ryland (1966) (Table 2b). In evaluating the results it is necessary to introduce the durations of the development stages and I am indebted to my colleague, Mr D. Harding, for advice on this point. The time T (days) to the end of a particular development stage from either laying or hatching has been expressed as

$$T = a + b \log_{10}\theta \qquad (1)$$

where θ = water temperature (°C). The values used for a and b are given in Table 3.

Evaluation of the data

The main objective in processing the data has been to follow through, from survey to survey, the development of particular batches of eggs. The information obtained from this first stage of the processing is then used as the starting point of further analysis as described below. A simplified flow chart of the first stage of the processing is shown in Figure 2. From the results of these calculations sets of distributions were deduced, each starting from a particular

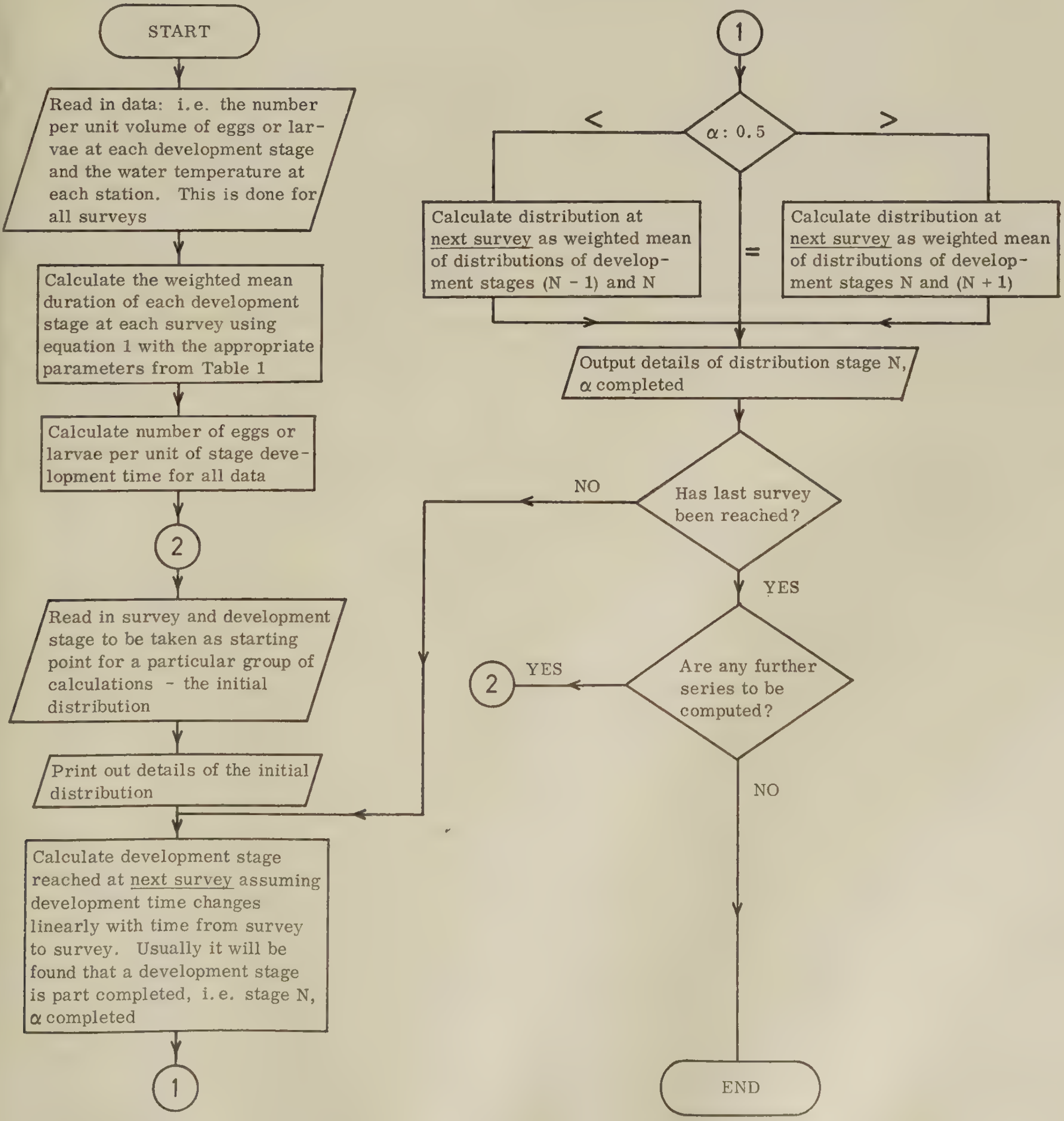

START
Read in data: i.e. the number per unit volume of eggs or larvae at each development stage and the water temperature at each station. This is done for all surveys
Calculate the weighted mean duration of each development stage at each survey using equation 1 with the appropriate parameters from Table 1
Calculate number of eggs or larvae per unit of stage development time for all data
2
Read in survey and development stage to be taken as starting point for a particular group of calculations - the initial distribution
Print out details of the initial distribution
Calculate development stage reached at next survey assuming development time changes linearly with time from survey to survey. Usually it will be found that a development stage is part completed, i.e. stage N, α completed
1
1
α : 0.5
<
>
=
Calculate distribution at next survey as weighted mean of distributions of development stages (N - 1) and N
Calculate distribution at next survey as weighted mean of distributions of development stages N and (N + 1)
Output details of distribution stage N, α completed
Has last survey been reached?
NO
YES
Are any further series to be computed?
YES
2
NO
END

Figure 2. Simplified flow chart of the first stage of processing of the plaice egg and larval data.

cruise and egg or larval development stage, and showing the resultant distribution at the time of subsequent cruises. A considerable number of sets of distributions can be produced in this way and, as examples Figures 3 and 4 show four sets for each of the years 1962 and 1969. In some cases parts of the outer contours on these distributions are shown by broken lines. These denote that the contours are on the outer edge of the area actually surveyed and less confidence can be put upon them. The worst case is probably cruise 5 of the 1962 data where a number of contours could not be closed to the northeast. In general the broken lines cover only a small fraction of the total circumferences of the distributions, so it is unlikely that this uncertainty can lead to appreciable errors in the conclusions reached below regarding the effect of diffusion on egg and larval dispersal. Consideration of the latter process was the subject of the second stage of the analysis.

The distributions are usually somewhat irregular in shape but, from the point of view of diffusion, the area within isolines is more important than the shape. Deviations from a circular pattern have therefore been ignored; for each isoline the area enclosed has been measured and the radius of the circle having the same area calculated. This is referred to below as the equivalent radius. This approximation has been used frequently by workers in diffusion, including Joseph and Sendner (1958), and it enables the distribution $N(r, t)$ to be represented at a particular time in terms of a single independent variable, the equivalent radius, r. It was expected that diffusion would cause $N(r, t)$ to change with time and this function was therefore examined from survey to survey by plotting the number of eggs or larvae per unit volume, henceforth called the concentration, against the equivalent radius.

Results for the year 1962

The results for this year provide a convenient basis for comparison with the 1969 results which are described later. Four sets of distributions for 1962 have already been mentioned (Fig. 3) and the corresponding variations of concentration with equivalent radius are shown in Figure 5. These results have the interesting property that, as plotted on a logarithmic-linear scale, they are to a close approximation straight lines whose slope shows little change from cruise to cruise. The same feature has been found in plaice egg and larval distributions measured in the Southern Bight in 1963 and also in the eastern Irish Sea in 1965. If this is indeed a general characteristic

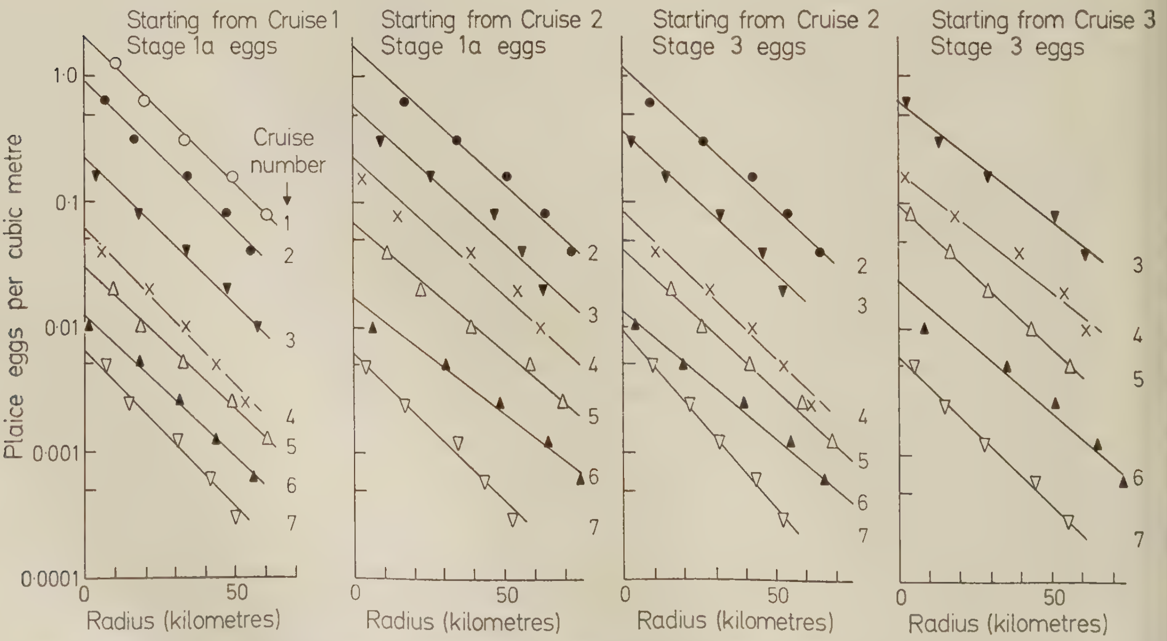
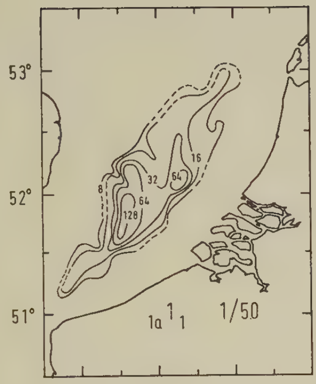
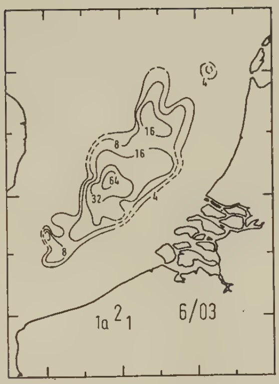


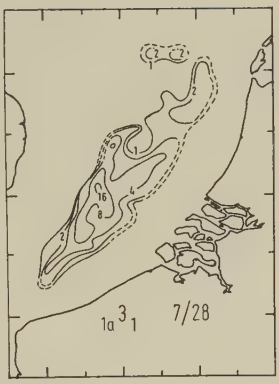
Figure 5. Variation of number of eggs/larvae per unit volume with equivalent radius for the 1962 distributions shown in Figure 3. Each line refers to the distribution at a particular cruise, the plotted points are at the contour levels of Figure 3.


53°
52°
51°
8
16
32
64
128
64

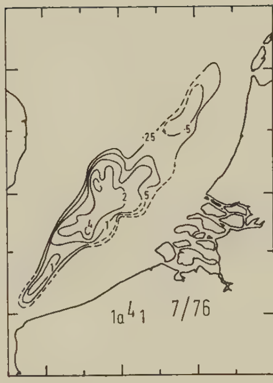
$1a^{1}_{1}$ 1/50


4
16
8
16
64
32
4
8

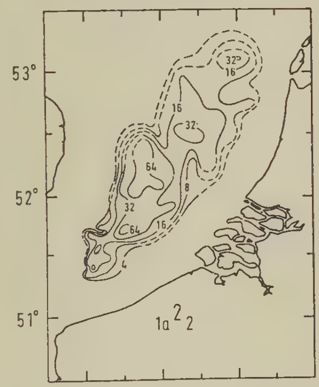
$1a^{2}_{1}$ 6/03



$1a^{3}_{1}$ 7/28



$1a^{4}_{1}$ 7/76


53°
52°
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16
16
32
64
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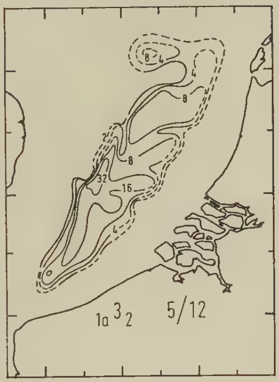
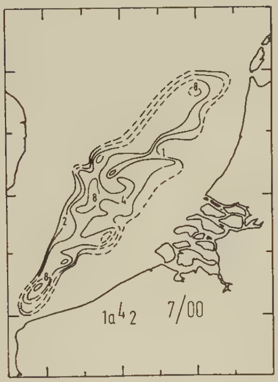
32
64
16
4

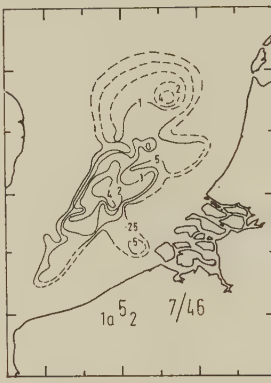
$1a^{2}_{2}$


8
4
4
8
2
8
32
16
4

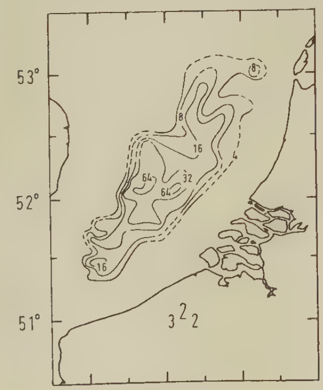
$1a^{3}_{2}$ 5/12



$1a^{4}_{2}$ 7/00



$1a^{5}_{2}$ 7/46


53°
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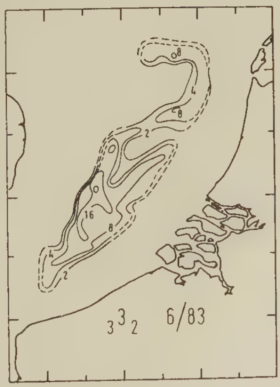
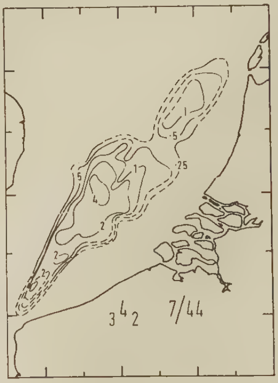
8
8
16
4
64
32
64
16

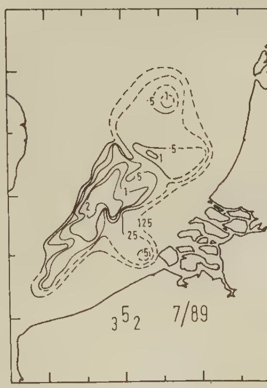
3^{2}_{2}



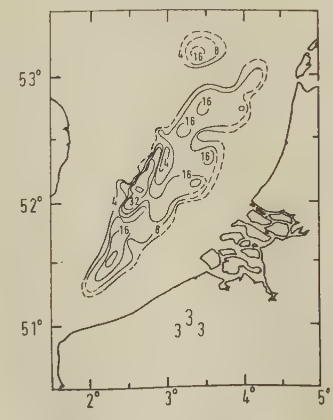
3^{3}_{2} 6/83



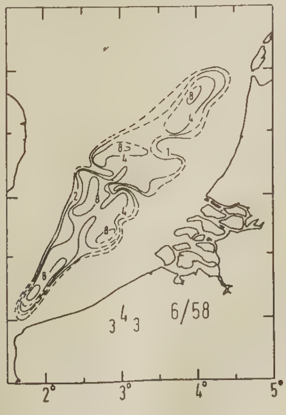
3^{4}_{2} 7/44


.5
1
.5
1
.5
1
2
125
25
.5

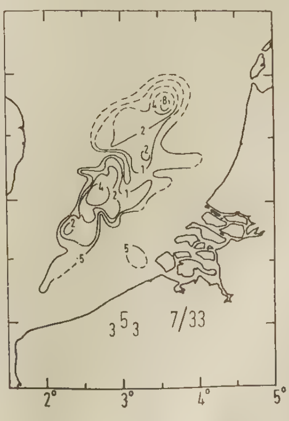
3^{5}_{2} 7/89


53°
52°
51°
2°
3°
4°
5°
16
8
16
16
16
4
16
32
4
16
8

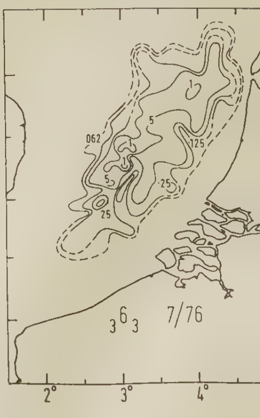
3^{3}_{3}


5°
2°
3°
4°
8
4
8
4
1
2
8
8
8

3^{4}_{3} 6/58


5°
2°
3°
4°
8
2
2
1
4
1
2
5
.5

3^{5}_{3} 7/33


2°
3°
4°
1
5
062
125
5
25
25

3^{6}_{3} 7/76

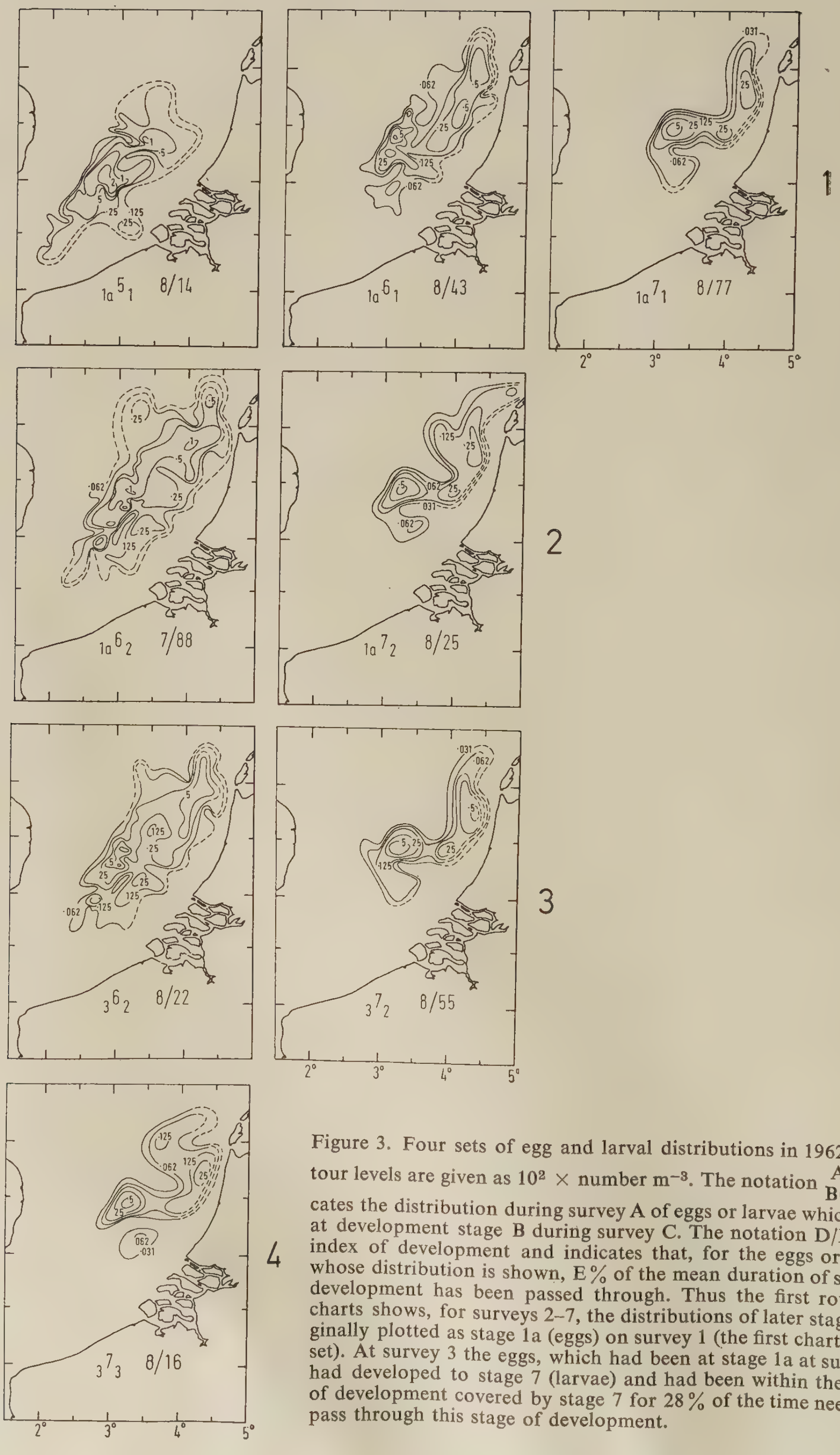
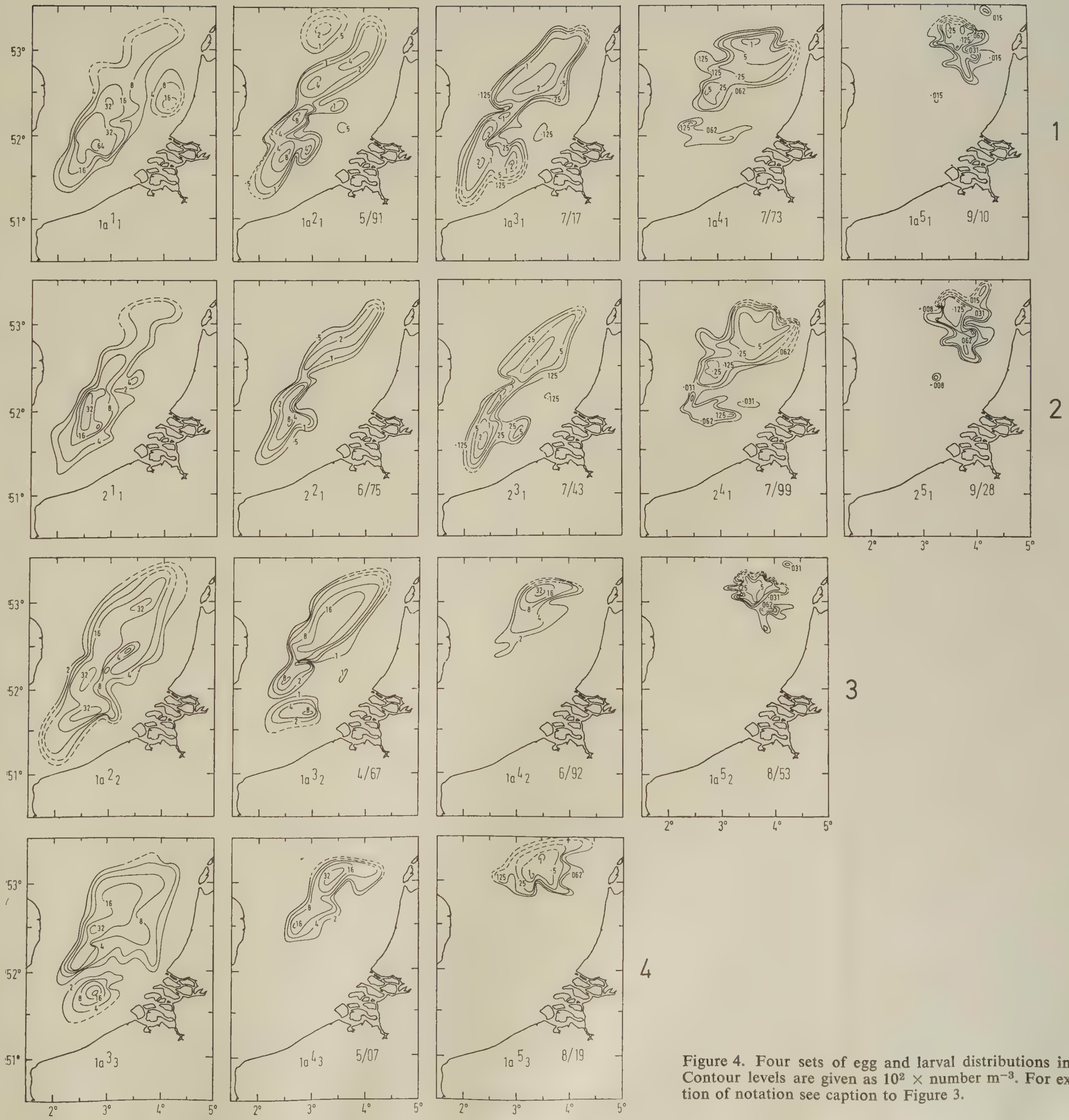


Figure 3. Four sets of egg and larval distributions in 1962. Contour levels are given as $10^2 \times$ number m^{-3}. The notation $\overset{A}{BC}$ indicates the distribution during survey A of eggs or larvae which were at development stage B during survey C. The notation D/E is an index of development and indicates that, for the eggs or larvae whose distribution is shown, E % of the mean duration of stage D development has been passed through. Thus the first row of 7 charts shows, for surveys 2–7, the distributions of later stages originally plotted as stage 1a (eggs) on survey 1 (the first chart of the set). At survey 3 the eggs, which had been at stage 1a at survey 1, had developed to stage 7 (larvae) and had been within the range of development covered by stage 7 for 28 % of the time needed to pass through this stage of development.



1
2
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53°
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51°
2°
3°
4°
5°
1a 1 1
1a 2 1 5/91
1a 3 1 7/17
1a 4 1 7/73
1a 5 1 9/10
2 1 1
2 2 1 6/75
2 3 1 7/43
2 4 1 7/99
2 5 1 9/28
1a 2 2
1a 3 2 4/67
1a 4 2 6/92
1a 5 2 8/53
1a 3 3
1a 4 3 5/07
1a 5 3 8/19

Figure 4. Four sets of egg and larval distributions in 1969. Contour levels are given as $10^2 \times$ number m^{-3}. For explanation of notation see caption to Figure 3.

of the distributions then, to a reasonable degree of approximation, they may be represented by an equation of the form

$$N(r, t) = N(O, t) \exp(-r/A), \qquad (2)$$

where $N(O, t)$ and A are parameters discussed further below.

Thus the spatial distribution of eggs and larvae is similar in form to the Joseph and Sendner diffusion equation

$$N(r, t) = N(O, t) \exp(-r/Pt), \qquad (3)$$

where P is known as the diffusion velocity.

The distribution represented by Equation (2) is determined by the two parameters $N(O, t)$ and A. The first of these depends on both diffusion and natural mortality of eggs and larvae but, if it is assumed that mortality is independent of concentration, then A will depend only on the rate of diffusion and time. Classification of the distributions in terms of A (Table 4) shows that, at least for the examples given, the value of A for a particular spawning of eggs changes surprisingly little in time. This is true even over the period of 8 weeks covered by the surveys, whereas from the Joseph and Sendner diffusion equation we should expect a significant and linear increase with time. The main variation in A is between different batches of eggs, spawned at different times, as demonstrated by comparison of results obtained in 1962 (Table 4) and 1963 (Table 5). For 1963 the first stage of the calculations has not been performed; so it is not possible to follow through the development in time of particular groups of eggs. Instead, the distributions of particular development stages have been used and these show clearly that in 1963, a much colder year, the distributions were all much tighter, and hence had smaller A values, and kept this tighter form throughout the period of development covered by the surveys.

Table 4. Values of the parameter A (km) in Equation (2) for the 1962 distributions shown in Figure 3

Starting distribution	Number of survey at which distribution measured						
	1	2	3	4	5	6	7
Survey 1 Stage 1a eggs	19·1	19·8	21·9	21·9	17·0	21·6	20·0
Survey 2 Stage 1a eggs		32·2	26·3	22·2	20·6	33·6	19·5
Survey 2 Stage 3 eggs		24·0	21·8	23·6	19·4	30·1	19·4
Survey 3 Stage 3 eggs			23·0	23·0	19·1	20·8	18·7

Table 5. Values of the parameter A (km) in Equation (2) for some 1963 distributions

Survey	Development stage			
	1a (eggs)	3 (eggs)	5 (eggs)	6 (larvae)
1	9·5	7·6	6·4	4·8
2	8·1	7·4	7·9	7·5
3	9·3	8·4	7·8	8·3

Results for the year 1969

For some of the 1969 results the dependence of $N(r, t)$ upon r follows the form of Equation (2) less closely than did the 1962 and 1963 results. This fact is illustrated in Figure 6 which shows that a few distributions deviated somewhat from a straight line graph, although most still follow Equation (2) quite closely. Hence, for most of the 1969 distributions the parameter A can be determined with the same confidence as for the earlier results, discussed above, but in a few cases the use of this parameter gives only a very approximate representation of the observed distribution. Table 6 gives the A values deduced for some of the 1969 surveys, with those cases where there was appreciable departure from Equation (2) given in parentheses. The values are generally intermediate between those for 1962 and 1963 but show some tendency for A to decrease as a distribution develops in time. This is the opposite of what would be expected if diffusion were a significant factor.

Evidence for the effect of diffusion on the distributions

It has been pointed out above that Equation (2) becomes the Joseph and Sendner diffusion equation if

Table 6. Values of the parameter A (km) in Equation (2) for the 1969 distributions shown in Figure 4

Starting distribution	Number of survey at which distribution measured				
	1	2	3	4	5
Survey 1 Stage 1a eggs	23	27·3	(22·1)	15·6	14·8
Survey 2 Stage 1a eggs		(17·4)	15·2	11·3	8·7
Survey 3 Stage 1a eggs			(18·3)	12·6	13·0
Survey 1 Stage 2 eggs	18·9	17·8	16·9	14·1	10·0

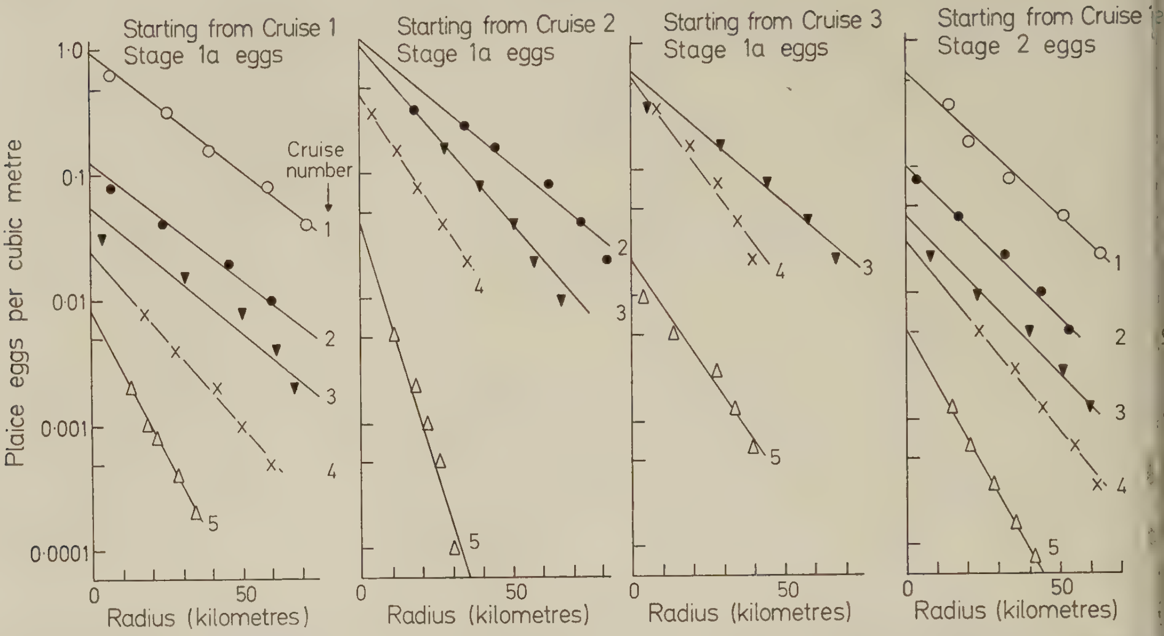


Figure 6. Variation of number of eggs/larvae per unit volume with equivalent radius for the 1969 distributions shown in Figure 4. Each line refers to the distribution at a particular cruise, the plotted points are at the contour levels of Figure 4.

the expression *Pt* is substituted for the parameter *A*. *P* is the diffusion velocity and Joseph and Sendner (1958) suggested that this should be of the order of 1 cm/s. Now the time between the mid-point of the first and last plankton surveys in 1962 was 60 days, so that over this interval the expression *Pt* should have increased by about 52 km. The values obtained for *A* that year (Table 4) were of the order 20 km, so that a very noticeable increase might have been expected. Even a value of *P* as low as 0·1 cm/s would have produced an increase of *Pt* of 5 km, which should have been detected. In 1963 the values of *A* were appreciably smaller than in 1962, but there is again no indication of an increase with time, and in 1969 *A* appeared to decrease slightly with time.

These results are consistent with the conclusion that at the scale of the plaice egg distributions diffusion was at a rate appreciably lower than that given by a diffusion velocity (*P*) of 0·1 cm/s. Alternatively, some biological process could mask diffusion: it is possible that mortality of eggs and larvae is always greater in the low concentration areas and that this just counterbalances the effects of diffusion. However, the simpler hypothesis is that the effects of diffusion and dependence of mortality on concentration are both small even though there might be some tendency for the two processes to cancel.

This hypothesis is quite consistent with all the results to the extent that in no case is there any evidence for a significant effect of diffusion. However the tendency for *A* to decrease in 1969 is surprising and the part played by medium scale advective effects has therefore been considered.

The influence of medium-scale advective effects

The analysis so far has dealt with concentration as a function of area. Changes in shape of the distributions will now be examined in a further attempt to discover the important factors controlling the development of the distributions. Consider, as examples, the first two sets of distributions shown in Figures 3 and 4. These are for the development of eggs which were stage 1a at the first survey in 1962 and for eggs which were stage 1a at the first survey in 1969. It is immediately clear that these distributions developed in markedly different ways. In the case of the 1962 group most of the eggs or larvae stayed in the central Southern Bight until the last two surveys. By the sixth survey, 49 days after the eggs had been spawned, and when they had developed to stage 7 (larvae), a movement to the north-east occurred. At the last survey some larvae had moved quite close in to the Dutch nursery grounds.

In contrast, the set of results in Figure 4 for 1969 shows that the initial distribution of eggs was more clearly divided with two well-separated areas of maximum concentration. As this distribution developed a greater part of it was located to the northeast of the area than was the case for the 1962 results. By the second survey the southwestern part of this distribution had split to have three maxima and the whole distribution had developed a neck at about latitude 52°20′N. This was further developed by the third survey, suggesting a movement of water from the adjacent coastal areas. At the fourth survey, 32 days from spawning of the eggs and when development had reached stage 7 (larvae), the main (northeastern) part of the distribution had moved to the northeast and the southwestern part, which had split at the previous survey, now appeared to have declined very considerably in numbers. At the last survey almost all larvae found were in the northeastern part of the area and some may have moved further to the northeast, out of the area actually surveyed. Development in 1962 and 1969 may thus be summarized by stating that in the earlier year movement of the plankton patch to the northeast was slow and as the larvae developed some moved inshore towards the Dutch coast. In contrast, in 1969 the distribution was more subdivided and few larvae remained in the southwest; eggs laid to the north of 52°20′N moved noticeably to the northeast and showed a less pronounced movement to the Dutch coast.

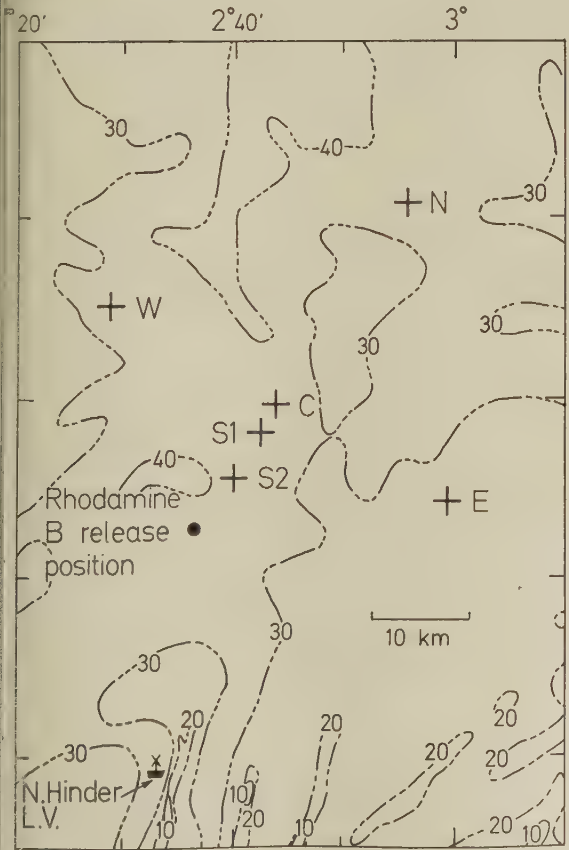


Figure 7. Positions of the moored current meters in January–February 1969 and of the Rhodamine-B release. Depth contours in m.

It appears from the above description that development of the 1969 distributions was influenced by circulation features significantly different from those existing in 1962. The 1969 surveys included hydrographic observations using moored current meters and the tracer Rhodamine-B and these observations are discussed first before considering evidence for differences in the hydrographic conditions in 1962 and 1969.

Hydrographic conditions in early 1969

The two hydrographic features most relevant to a consideration of plaice egg dispersal are the residual circulation and the rate of diffusion. The first of these was investigated during a part of the 1969 survey using an array of recording current meters moored in the centre of the main plaice spawning area; diffusion rates were measured directly using the tracer Rhodamine-B. The current meters were moored at 6 stations (Fig. 7) covering an area measuring 38 × 33 km in the central Southern Bight and were in position from 25 January to 4 February 1969.

The residual circulation shown by the current meters

At a first impression the current meter results suggest a confused and complex pattern of residual circulation (Fig. 8). However, on closer examination much of the apparent complexity is found to be associated with the component of predicted water movements that is normal to the main direction of the tidal oscillation. If a current meter is placed in a sinusoidally and reciprocally oscillating stream in which the peak velocity is U and where the current direction is confined to one line, a false residual will be shown normal to the direction of oscillation and of magnitude $(U \sin\alpha)/\pi$, if the calibration error for the flood direction differs by an amount α from that for the ebb. Thus for $\alpha = 1°$ and $U = 50$ cm/s the spurious residual would be 0·25 cm/s. In practice tidal oscillations are not confined to a single direction but usually have an elliptical form. In the Southern Bight the ellipticity is fairly high, so that the mean hourly velocities over 4 hours cover a range of direc-

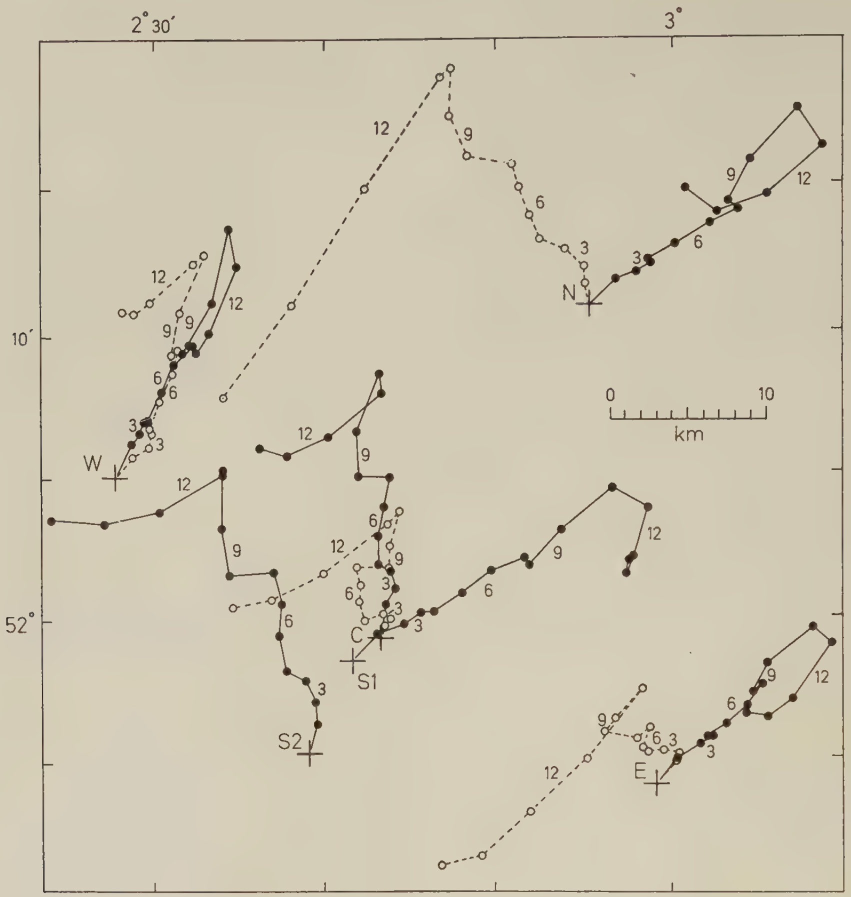


Figure 8. Residual flow deduced from current meters moored near the surface (●) and near the bottom (○) for 14 tides starting 0020 h on 28 January 1969. Numbers beside line denote respective tide.

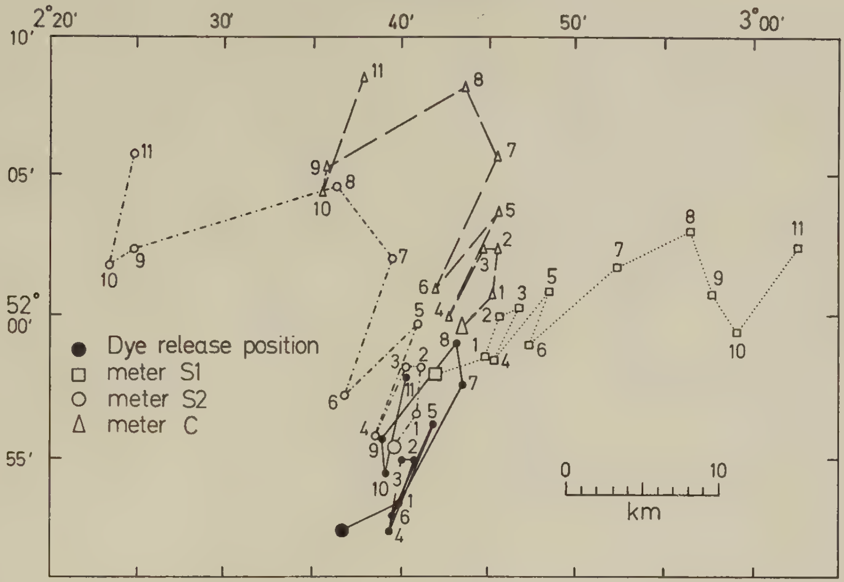
tions of about 30°. Current meter calibrations are carried out at 10° and 20° intervals so that the major portion of the tide will involve a very small number of individual direction calibration values. Examination of such calibration data suggests that any inherent errors often change slowly with angle. Thus a spurious residual could well occur in practice although, because the tidal oscillation is elliptical and the direction error may vary with angle, the magnitude may be somewhat smaller than derived above. On the other hand, peak tidal velocities in the Southern Bight are usually appreciably greater than 50 cm/s and the current meter compass resolution is quoted as ±2°, so that spurious residuals of 1 cm/s could occur and this is of the same order of magnitude as typical drift velocities, which are normally around 3 cm/s. The components of predicted residuals that are normal to the main direction of tidal flow are therefore to be treated with caution. Figure 9 shows the movement, from survey to survey, of the centre of the Rhodamine-B patch and the residuals calculated over the same intervals of time from the Eulerian current meter results, and Figure 10 compares the components of these residuals (w) and (m), for Rhodamine and current meters respectively, in directions along and normal to the main tidal axis. For component movements along the main tidal axis regression analysis gives a relation:

$$w = 0{\cdot}97\, m + 0{\cdot}12$$

with a correlation coefficient of 0·96. For movements normal to the tidal axis the corresponding relation is:

$$w = 0{\cdot}61\, m + 0{\cdot}64$$

with a correlation coefficient of 0·44. Direction errors of the meters could well have contributed


2°20'
30'
40'
50'
3°00'
10'
05'
52° 00'
55'
● Dye release position
□ meter S1
○ meter S2
Δ meter C
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10
km

Figure 9. Comparison, from survey to survey, of movement of Rhodamine-B patch with the corresponding residuals calculated from the results of three current meters moored in the upper part of the water column and near the patch.

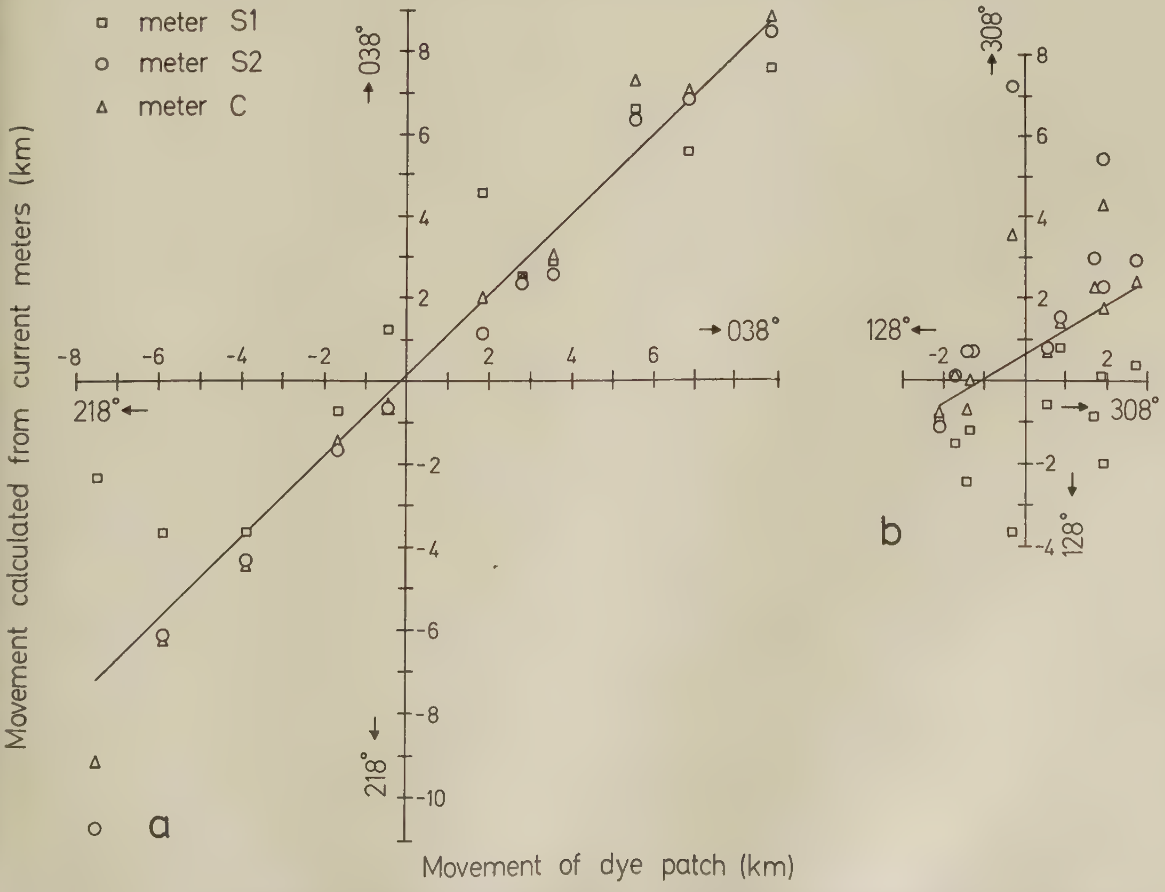


Figure 10 (a) & (b). Comparison of dye patch movements with current meter results, both resolved (a) along and (b) across the main tidal axis. The positions of the meters are shown in Figure 7.

to these differences. All current meter residuals resolved along and normal to the main tidal direction are shown in Figures 11 and 12. For velocity components along the tide, the meters, and especially those in the upper part of the water column, show good agreement, even though they were up to 30 km or more apart. The transverse tidal components also show a high degree of coherence, but in this case there are persistent differences between individual records, which could be due partly to compass calibration errors, although there could have been other contributory factors.

The overall degree of coherence shown by these results suggests that some common cause was influencing the residual flow over the area of the current meter array. The relationship between surface wind and residual flow was therefore investigated. The northeasterly component of the residual flows showed a significant relationship to the southwesterly component of the wind during each tidal cycle (Fig. 13). One hundred and fifteen surface and 71 near-bottom observations gave correlation coefficients of 0·64 and 0·63 and the regression equations

$$u = -0{\cdot}36 + 0{\cdot}53\,v \qquad (4)$$

and

$$u = -1{\cdot}93 + 0{\cdot}55\,v \qquad (5)$$

for the upper and lower meters respectively. Here u = residual drift of water (cm/s) and v = wind speed (m/s). A greatly reduced dependence was found between the northwesterly component of the residual and the southeasterly component of the wind (Fig. 13), the correlation coefficients being 0·11 and 0·49 and the regression lines $u = 0{\cdot}24 + 0{\cdot}06\,v$ and $u = -0{\cdot}66 + 0{\cdot}19\,v$ for upper and lower meters respectively. It seems probable that the correlation between the northeasterly flow and the southwesterly wind results not so much from a direct wind-water effect in the Southern Bight itself but indirectly from the influence of wind over a larger area on the general circulation as indicated by flow of water through the Dover Strait. The coefficients of wind velocity in Equations (4) and (5) above are about one fifth of the corresponding coefficient given by Bowden for flow through the Strait (Bowden, 1956). This ratio is close to that obtained below when flow through the Strait deduced from telephone cable data is compared with movement in the central Southern Bight as shown by the Rhodamine-B patch.

The following discussion is concerned mainly with the component residuals along the tide since the transverse components are of a lower accuracy. With this stipulation the moored current meters show that the residual drift was remarkably uniform over the area of the array and this drift agreed closely with that of the Rhodamine-B patch (Figs. 9 and 10). This implies that in this area the component of the Stokes velocity along the main tidal axis is small. The records obtained at current meter stations S2, C and N (Fig. 7) have been used to estimate a value for the Stokes velocity along the line joining these meters. The procedure involved a harmonic analysis to select the amplitude and phase of the mean M_2 component for the same period of each record. The Stokes velocity was then evaluated as $\overline{\int u\,dt\,\frac{\delta u}{\delta x}}$, where t denotes time and x distance along the line of the meters. This procedure thus followed the work of Longuet-Higgins (1969) and Dooley (1974). For meters spaced so closely this procedure demands very accurate timing of the meters. The amplitudes of the M_2 oscillations derived for the three positions were the same to within ±1 cm/s. For the region between S_2 and C, which is the area of the Rhodamine patch, the Stokes velocity was calculated to be less than 0·3 cm/s. Further to the northeast, between meters C and N, the predicted value was about 0·7 cm/s. Although great accuracy cannot be claimed for these results they do provide some support for the other results discussed above.

The measurement of diffusion

The interpretation of the plaice larval distributions in terms of diffusion has been described above. A study of the development of a Rhodamine-B patch also formed a major part of the 1969 investigations and provided a further insight into the diffusion process in the Southern Bight.

The fluorescent dye Rhodamine-B has been used in many experiments designed to measure rates of diffusion in the sea. However, because of the cost and the difficulty of releasing a sufficiently large quantity of tracer, direct measurements at the scale of the egg and larval distributions are almost impossible. For these practical reasons the tracer measurements could cover scales only up to about 10 km and cannot therefore be applied directly to the larger plankton distributions. However, the results do help to resolve the relative contributions to horizontal diffusion from horizontal turbulence on the one hand and vertical shear diffusion associated with the tidal oscillation on the other. Since only the first of these processes may be expected to be scale-dependent, knowledge of their relative importance is fundamental to the estimation of rates of diffusion at scales greater than those covered by the actual measurements.

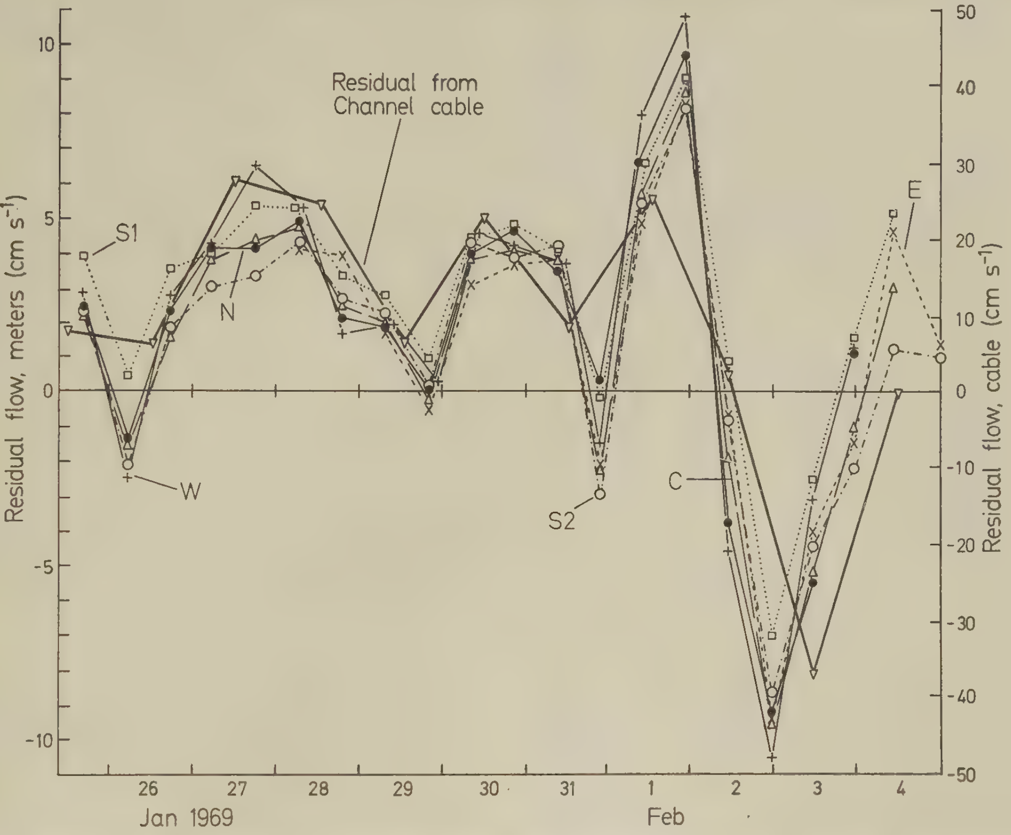


Figure 11. Residual flow, measured by the current meters, resolved along the main tidal direction. The daily residual flow calculated from the Channel telephone cable data is also shown (see page 246). The positions of the meters are shown in Figure 7.

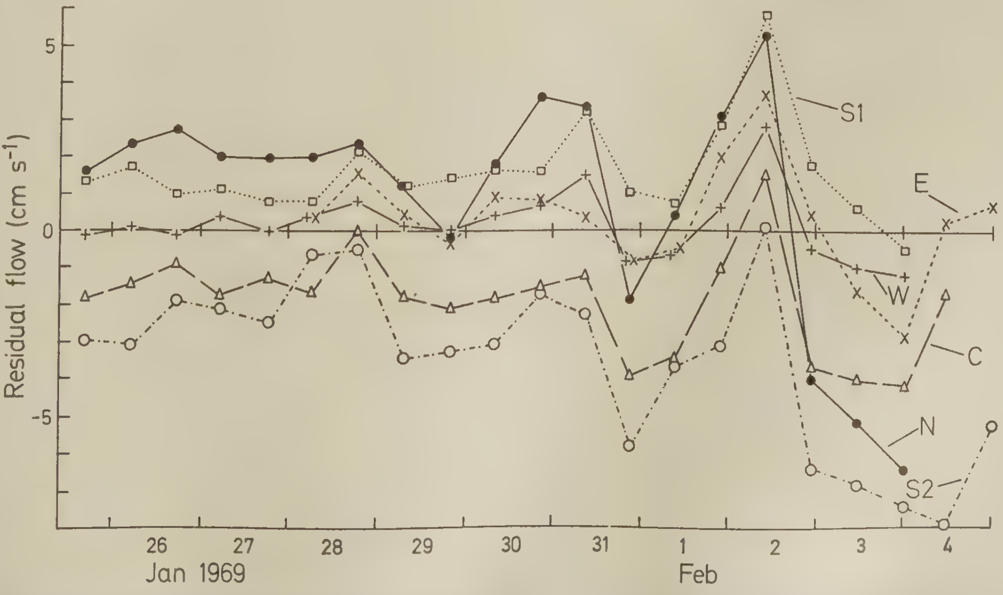


Figure 12. Residual flow measured by the current meters resolved normal to the main tidal direction. The positions of the meters are shown in Figure 7.

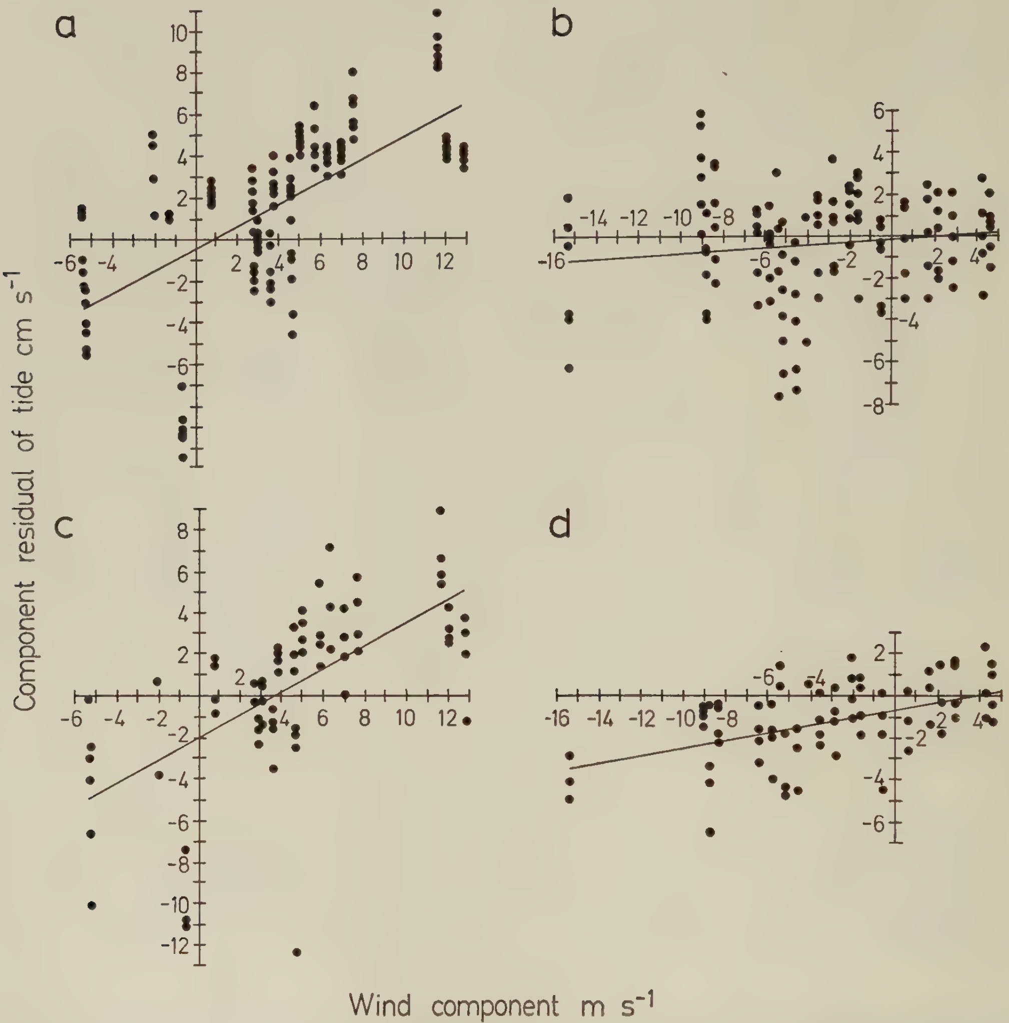


Figure 13. Relationship for current meters in the upper part of the water column between (a) northeasterly (along the tide) flow and the southwesterly component of the wind during each tidal cycle and (b) southeasterly (across the tide) flow and the northwesterly wind component. The corresponding relationships for meters in the lower part of the water column are shown in (c) and (d) respectively.

The diffusion survey was carried out by the Ministry of Agriculture, Fisheries and Food's research vessels, "Clione" and "Corella", both medium-sized vessels of a little over 40 m in length. It was intended that the dye should be released as a point source close to the surface at a position near the centre of the egg and larval distributions, where the water depth was about 36 m. The release was made by "Corella" at 1435 GMT on 27 January 1969 and was at 51°53′N 02°36′E (Fig. 7). During the release the wind was southwest × south force 5 and the sea state 3. Discharge of the dye occupied a total period of 22 min so that a streak rather than a point source was produced. Thirty minutes after commencement of the discharge the dye formed a red patch measuring at the surface about 300 m by 30 m. During the night following the release the two survey vessels stayed near to, but clear of, the dye patch and the first of 11 surveys of the dye distribution was carried out the following morning. The times of these surveys are given in Table 7. The survey procedure was for the ships to make a number of intersections through the patch; in some cases both ships worked together, starting, as far as possible, at opposite ends of the distribution and then working their way towards the centre. Other surveys involved only one ship which worked its way from one end of the patch to the other. All survey tracks were corrected for gross

Table 7. Times and summary of results of Rhodamine-B surveys, 28 January–4 February 1969

Survey	Time and date of survey (GMT)	Time after release (h)	Effective depth (m)	$10^{-4}\,K_x$ cm²/s	$10^{-3}\,K_y$ cm²/s
1	1059 28 Jan	21	42·5	5·2	2·7
2	1319 28 Jan	23	41·7	3·6	3·9
3	0429 29 Jan	38	28·9	5·7	5·3
4	0759 29 Jan	42	24·3	4·8	4·3
5	1429 29 Jan	48	29·5	4·6	7·2
6	0959 30 Jan	67	28·1	4·9	7·4
7	0229 31 Jan	84	32·5	5·4	7·5
8	1529 1 Feb	121	37·5	6·1	7·4
9	2109 3 Feb	175	29·3	6·5	6·9
10	1459 4 Feb	192	30·1	4·3	7·9
11	1809 4 Feb	196	27·4	6·6	7·8

water movement over the survey period by using the velocity records obtained from the current meters moored in the area. Thus the tracks used in the evaluation of these results were drawn relative to a frame of reference moving with the water.

Results of the diffusion experiment

The Rhodamine distributions deduced from the survey results were generally smooth and approximately elliptical in shape and have therefore been analysed along major and minor axes chosen as shown in Figures 14 to 22. The comparative simplicity of the distributions suggests that moderate-scale turbulence was of little importance in the area at the time of the surveys; an observation that is all the more significant because they were produced over a period which included some quite rough weather. Table 8 gives the wind recorded at the North Hinder lightvessel, 51°39′N 02°34′E (see Fig. 7), and shows that for a little over 2 days following the release of Rhodamine the wind speed held fairly steady at about 13 kn. After this initial period there was a general increase in wind strength and the lightvessel records show four periods when 25 kn was exceeded. Over the same total period the maximum height of sea waves noted at the North Hinder was 3 m and the maximum swell 1·5 m. The survey ships were usually closer to the dye patch than the North Hinder and recorded some higher wind velocities. On a number of occasions "Clione" noted wind speeds greater than 30 kn and on 1 February recorded gusts of up to 60 kn.

Some check on the reliability of the results is provided by evaluating the mass of Rhodamine per unit depth represented by each survey. Alternatively this result can be expressed as an effective depth of mixing, i.e. the depth that would be needed to account for the total mass of dye released. The results of these calculations (Table 7) show that even by the first survey the effective depth was of the order of the actual depth in the area and there was comparatively little variation in this quantity over the total period covered by the surveys. In order that the dye should have mixed almost uniformly throughout the depth by the first survey the vertical diffusion coefficient must have been greater than 50 cm²/s.

The elliptical form of the distributions has been noted above. For diffusion in two dimensions with constant diffusion coefficients K_x and K_y the distribution of concentration $S(x, y, t)$ is given by

$$S(x, y, t) = M/[4\pi Ht(K_xK_y)^{0\cdot 5}] \times \\ \times \exp\{-[x^2/(4K_xt) + y^2/(4K_yt)]\} \tag{6}$$

where M is the mass of substance,
H is the water depth,
x and y are space coordinates relative to the principal axes
and t is time.

Table 8. Wind speed and direction at the North Hinder lightvessel during the Rhodamine-B experiment

Date (1969)	0000 wind speed (kn)	0000 wind direction (true)	0600 wind speed (kn)	0600 wind direction (true)	1200 wind speed (kn)	1200 wind direction (true)	1800 wind speed (kn)	1800 wind direction (true)
27 Jan	13	210	13	200	13	200	13	210
28 Jan	13	180	13	180	13	180	13	200
29 Jan	13	300	13	320	13	290	13	300
30 Jan	13	270	13	260	18	240	24	230
31 Jan	24	240	30	250	30	260	24	290
1 Feb	13	290	13	250	18	210	24	210
2 Feb	24	250	24	250	24	320	30	310
3 Feb	30	320	18	320	13	30	18	10
4 Feb	13	20	13	330	13	350	9	310

Wind speeds based on an original record in terms of Beaufort number.

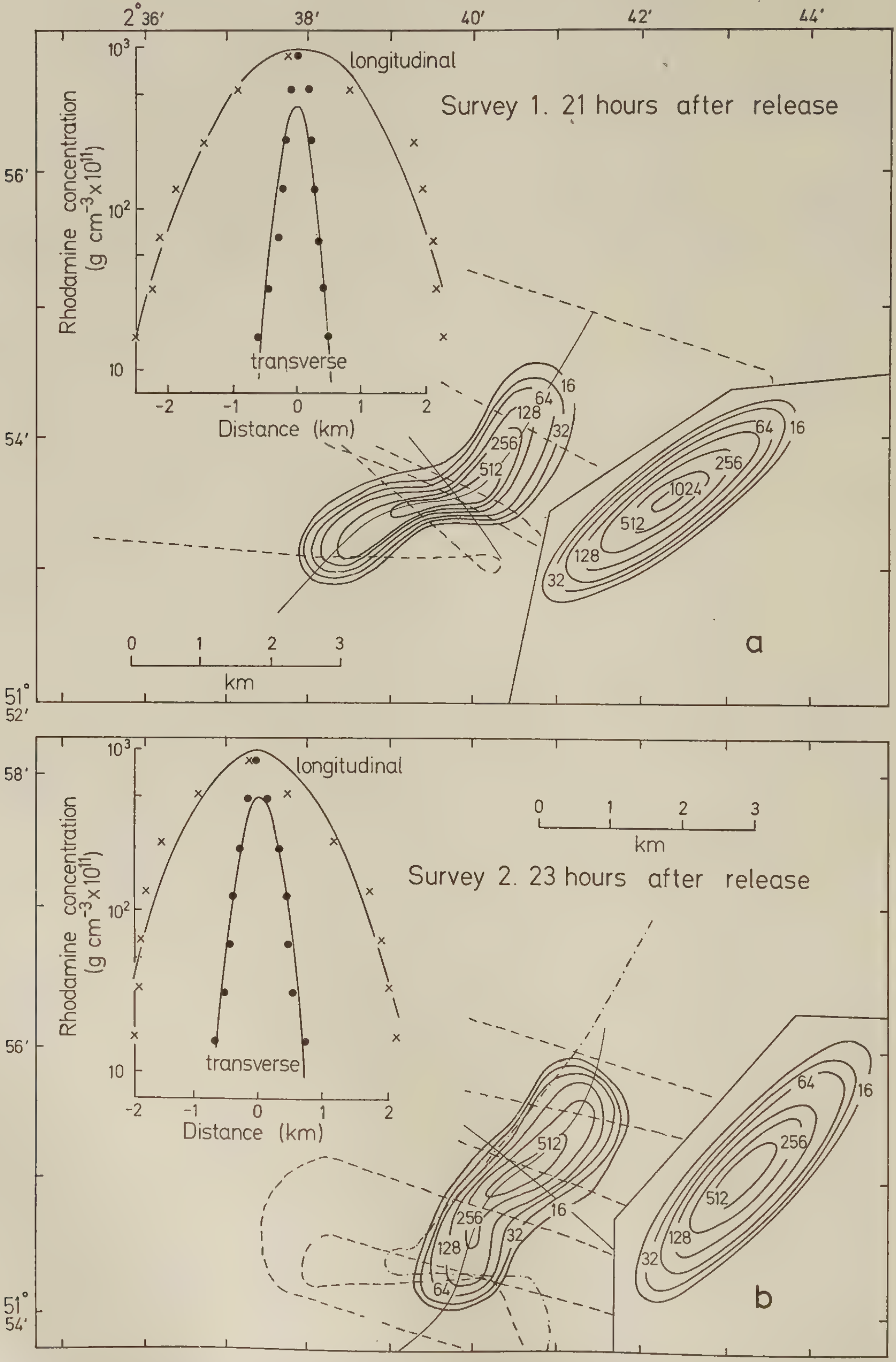

2°36'
38'
40'
42'
44'
56'
54'
51° 52'
10³
10²
10
Rhodamine concentration (g cm⁻³x10¹¹)
longitudinal
transverse
-2
-1
0
1
2
Distance (km)
Survey 1. 21 hours after release
16
64
128
256
512
32
1024
0 1 2 3
km
a
58'
56'
51° 54'
Survey 2. 23 hours after release
b

Figure 14 (a) & (b). Distributions measured in January 1969 (a) 21 and (b) 23 h after the release of Rhodamine-B. Contour levels are $10^{11} \times$ concentration in units of g cm^{-3}. The Gaussian curves were fitted to the distributions along the longitudinal and transverse axes shown by solid lines and the insets show the corresponding horizontal distributions obtained from the mathematical model assuming that eddy diffusion is horizontally isotropic and that the horizontal and vertical coefficients of eddy diffusion are 10^3 cm^2/s and 10^2 cm^2/s respectively. The broken lines show the courses of the survey vessels.

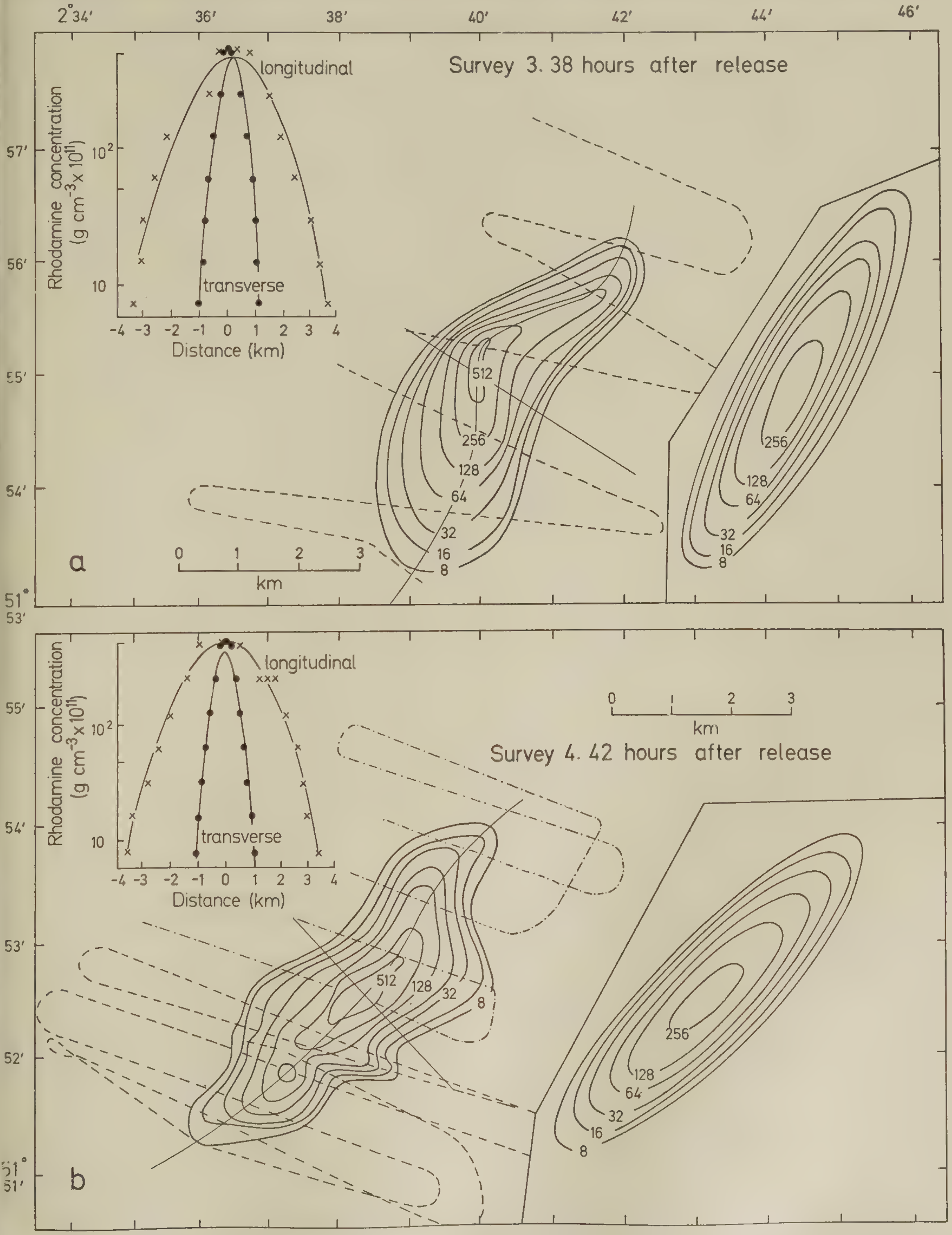

2°34′
36′
38′
40′
42′
44′
46′
57′
56′
55′
54′
51°
53′
Survey 3. 38 hours after release
longitudinal
transverse
Rhodamine concentration (g cm^{-3} x 10^{11})
10^2
10
-4 -3 -2 -1 0 1 2 3 4
Distance (km)
512
256
128
64
32
16
8
a
0 1 2 3
km
55′
54′
53′
52′
51°
51′
Survey 4. 42 hours after release
b

Figure 15 (a) & (b). Distributions measured in January 1969 (a) 38 and (b) 42 h after the release of Rhodamine-B. For further explanation see caption to Figure 14.

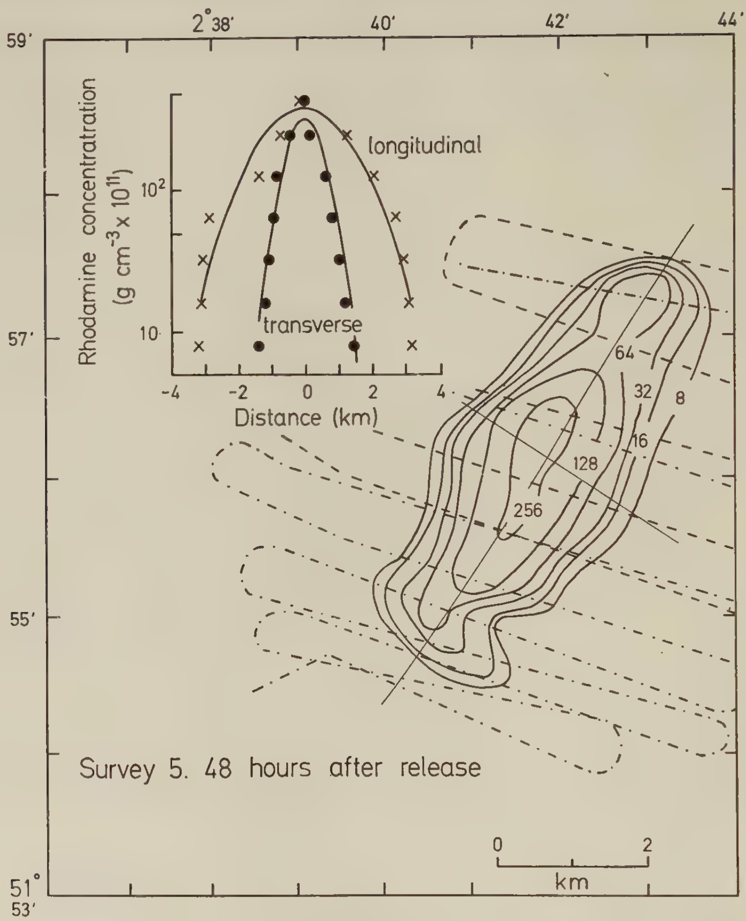


Figure 16. Distribution measured in January 1969 48 h after the release of Rhodamine-B. Contour levels are 10^{11} × concentration in units of g cm^{-3}. The Gaussian curves were fitted to the distributions along the longitudinal and transverse axes shown by solid lines. The broken lines show the courses of the survey vessels.

Gaussian curves, defined by Equation (6), were fitted along the principal axes (Figs. 14 to 22); the longitudinal and transverse diffusion coefficients K_x and K_y so derived are given in Table 7.

Since it is often supposed that diffusion in the open sea follows a law assuming a diffusion rate increasing with scale it is noteworthy that Equation (6) does indeed represent the results so well in terms of the individual distributions along the principal axes (Figs 14 to 22) and that such small variations in K_x and K_y were measured over the period of the experiment. It has been pointed out elsewhere (Talbot and Talbot, 1974) that the rate of decay of the maximum concentration depends more strongly on time than suggested by Equation (6), but that this may be largely explained if allowance is made for the variation of the amplitude of the tidal oscillation over the period of the experiment and the assumption made that the diffusion coefficient is linearly related to the peak tidal velocity.

From the results described above the ellipticity of each distribution was calculated as $(K_y/K_x)^{0.5}$. These values were compared with those derived assuming a linear relationship between the diffusion coefficients and the tidal velocity recorded at one of the moored current meter stations. In most cases the ellipticity was found to be greater than that to be expected if the diffusion coefficients were linearly related to the water velocities. This result confirms that the tidal oscillation is important and has a much greater influence on the diffusion process than horizontal turbulence, which would not produce markedly elliptical distributions. The result also suggests that the relationship between the diffusion coefficient and

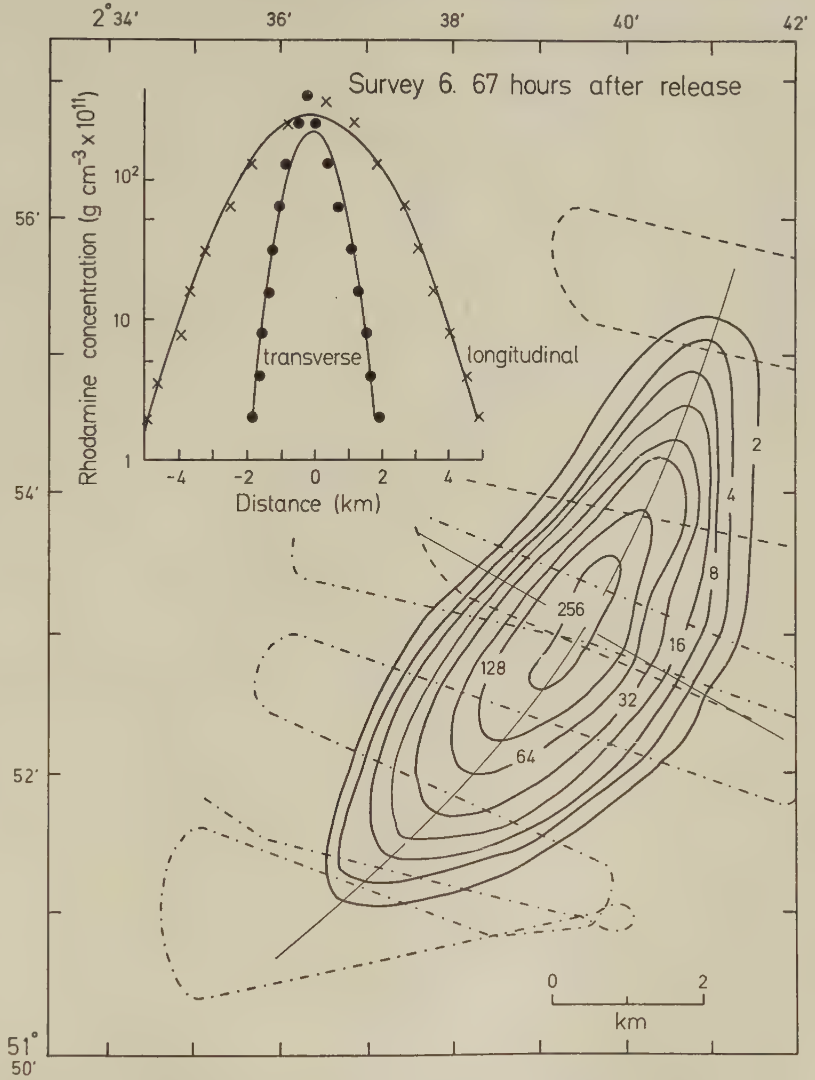

2°34'
36'
38'
40'
42'
Survey 6. 67 hours after release
Rhodamine concentration (g cm^{-3} x 10^{11})
10^2
10
1
-4
-2
0
2
4
Distance (km)
transverse
longitudinal
56'
54'
52'
51°
50'
2
4
8
16
32
64
128
256
0
2
km

Figure 17. Distribution measured in January 1969 67 h after the release of Rhodamine-B. For further explanation see caption to Figure 16.

the tidal velocity may be stronger than a direct proportionality. The interaction of vertical mixing and vertical current shear to produce vertical shear diffusion under conditions found in areas like the southern North Sea was further examined, using a mathematical model in three spatial dimensions as described below.

The vertical shear diffusion process in the southern North Sea

Two-dimensional analyses of diffusion have been published by Bowden (1965) and Okubo (1967). Bowden's analysis was restricted to the condition that the time (H^2/K_z) taken for mixing through the vertical water column (H) was short compared to the tidal period (T), i.e.

$$T \gg (H^2/K_z)$$

where K_z is the coefficient of vertical diffusion.

Okubo also considered the case where

$$T \ll (H^2/K_z)$$

but assumed a linear velocity profile.

No solution was proposed for the intermediate case, where

$$T \simeq (H^2/K_z). \qquad (7)$$

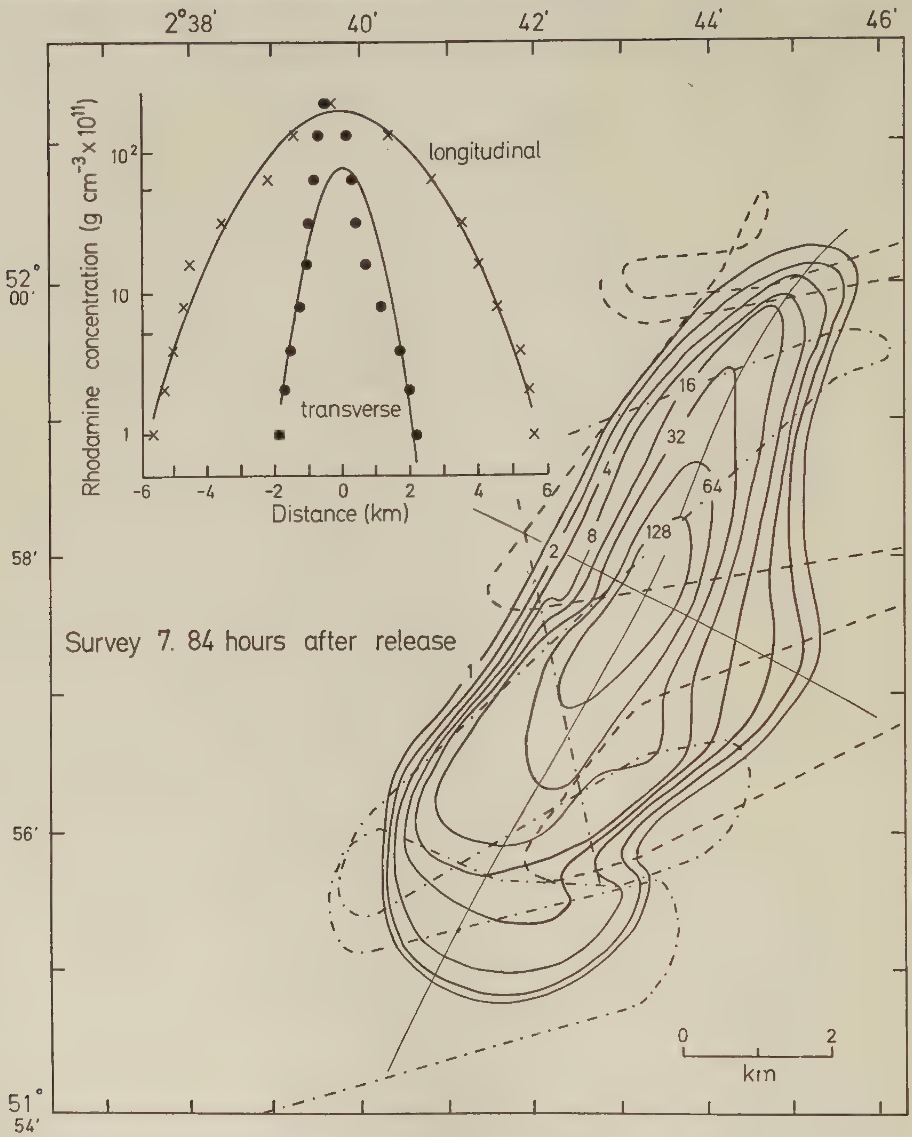

2°38'
40'
42'
44'
46'
52° 00'
58'
56'
51° 54'
Rhodamine concentration (g cm^{-3} x 10^{11})
10^2
10
1
-6
-4
-2
0
2
4
6
Distance (km)
longitudinal
transverse
Survey 7. 84 hours after release
1
2
4
8
16
32
64
128
0
2
km

Figure 18. Distribution measured in January 1969 84 h after the release of Rhodamine-B. For further explanaion see caption to Figure 16.

A recent analysis by Nihoul (1972) extended Bowden's treatment to three dimensions but was otherwise subject to the same restrictions.

In the Southern Bight the water depth and the likely value of the vertical mixing coefficient are such that Equation (7) may well apply. Since no analytic solution of the diffusion equation is available for this condition a numerical solution has been attempted. Both two- and three-dimensional forms have been used. In the following the three-dimensional analysis will be discussed since this permits a more complete representation of the results.

The general form of the diffusion equation is

$$\frac{\delta S}{\delta t} + u\frac{\delta S}{\delta x} + v\frac{\delta S}{\delta y} + w\frac{\delta S}{\delta z} =$$

$$\frac{\delta}{\delta x}\left(K_x\frac{\delta S}{\delta x}\right) + \frac{\delta}{\delta y}\left(K_y\frac{\delta S}{\delta y}\right) + \frac{\delta}{\delta z}\left(K_z\frac{\delta S}{\delta z}\right). \qquad (8)$$

Initially it was decided to exclude vertical advection and to assume values for the diffusion coefficients independent of the spatial coordinates.

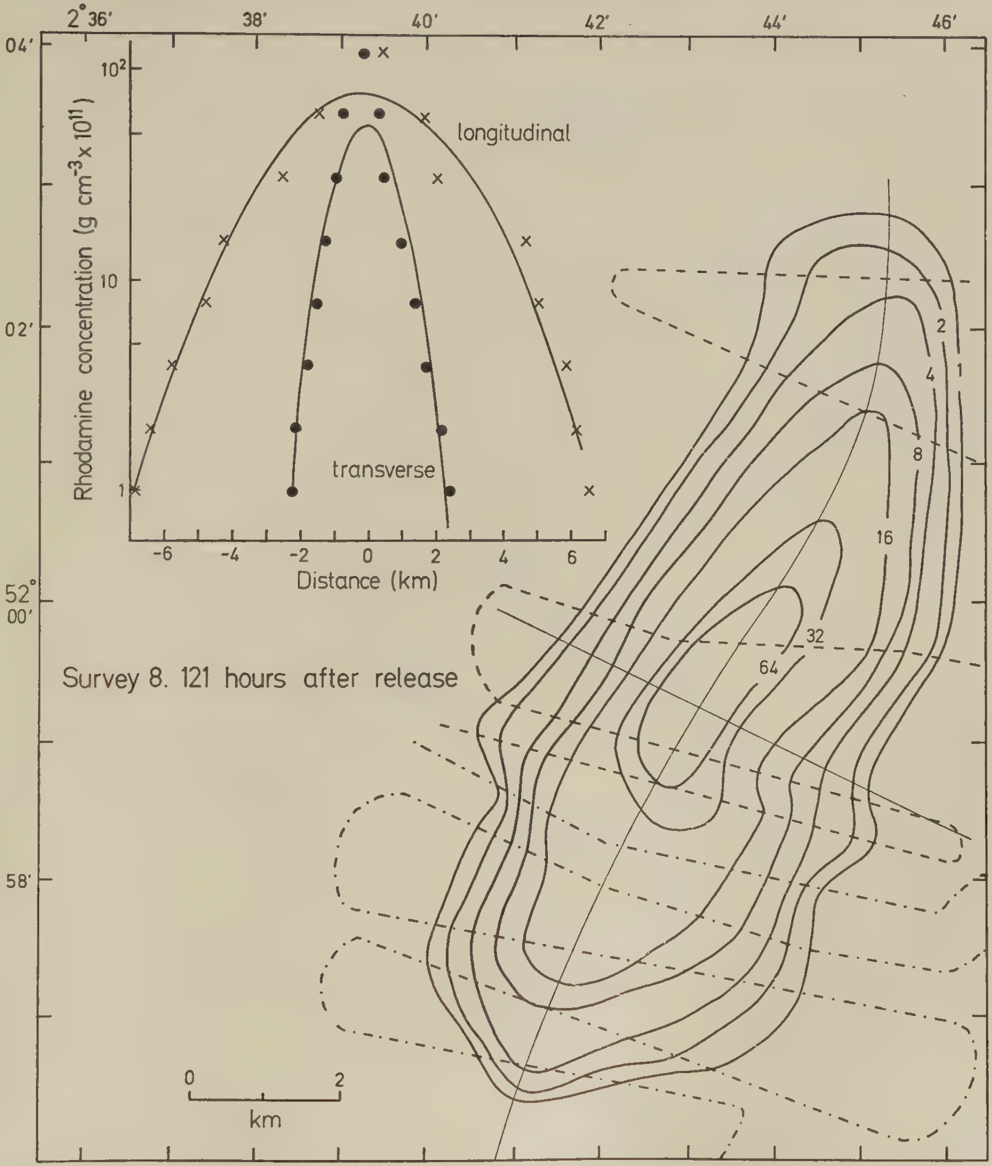

2°36'
38'
40'
42'
44'
46'
04'
02'
52° 00'
58'
10²
10
1
Rhodamine concentration (g cm⁻³ x 10¹¹)
longitudinal
transverse
-6
-4
-2
0
2
4
6
Distance (km)
Survey 8. 121 hours after release
2
1
4
8
16
32
64
0
2
km

Figure 19. Distribution measured in January 1969 121 h after the release of Rhodamine-B. For further explanation see caption to Figure 16.

The equation thus became

$$\frac{\delta S}{\delta t}+u\frac{\delta S}{\delta x}+y\frac{\delta S}{\delta y}=K_x\frac{\delta^2 S}{\delta x^2}+K_y\frac{\delta^2 S}{\delta y^2}+K_z\frac{\delta^2 S}{\delta z^2}. \quad (9)$$

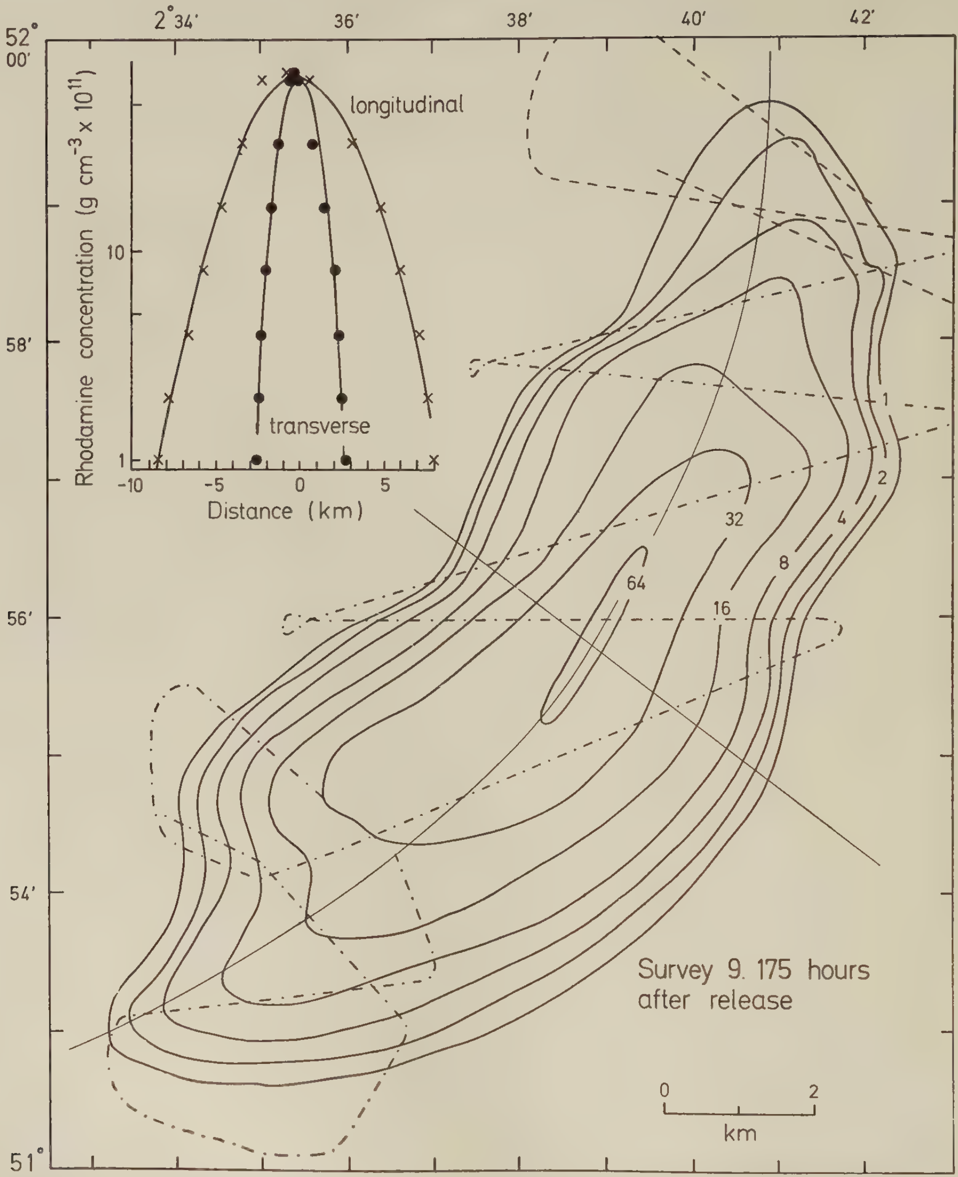
An elliptical tidal oscillation was assumed with sinusoidal components given by

$$u(z, t) = U(z/H)^N \sin(2\pi t/T)$$
$$v(z, t) = V(z/H)^N \cos(2\pi t/T) \quad (10)$$

and a van Veen vertical velocity profile with $N =$ 0·1923. It was also assumed that there was no phase change of the tidal components with distance either horizontally or vertically. Although the main interest is in the oscillatory terms provision was also made for steady components of the current field.

In solving Equation (9) numerically little difficulty was experienced in representing the non-advective terms such as $K_x/(\delta^2 S/\delta x^2)$. In finite difference form these were expressed

$$K_x/(\Delta x)^2(S_{x-1} - 2S_x + S_{x+1}).$$



52° 00′
2°34′
36′
38′
40′
42′
58′
56′
54′
51° 52′
Rhodamine concentration (g cm^{-3} x 10^{11})
10
1
-10
-5
0
5
Distance (km)
longitudinal
transverse
1
2
4
8
16
32
64
Survey 9. 175 hours after release
0
2
km

Figure 20. Distribution measured in January 1969 175 h after the release of Rhodamine-B. For further explanation see caption to Figure 16.

Representation of the advective terms proved more difficult: explicit and implicit solutions of the equation were attempted but both introduced unrealistic levels of numerical diffusion. In order to avoid this the following approach was adopted. Movement in the x and y directions was simulated by calculating the component displacements at each time step, $u_t \Delta t$ and $v_t \Delta t$. This calculation was performed for the time interval from $(t - \Delta t/2)$ to $(t + \Delta t/2)$. If, at time $(t + \Delta t/2)$, that is to say half-way through the time step t to $(t + \Delta t)$, the displacement is greater than half a grid spacing then the whole array at this level is moved a whole number of grid spaces to bring it to the nearest position to that calculated. Any balance in the displacement term is then carried forward to the next time step. Using this method no numerical diffusion is generated in any horizontal plane by the simulation of

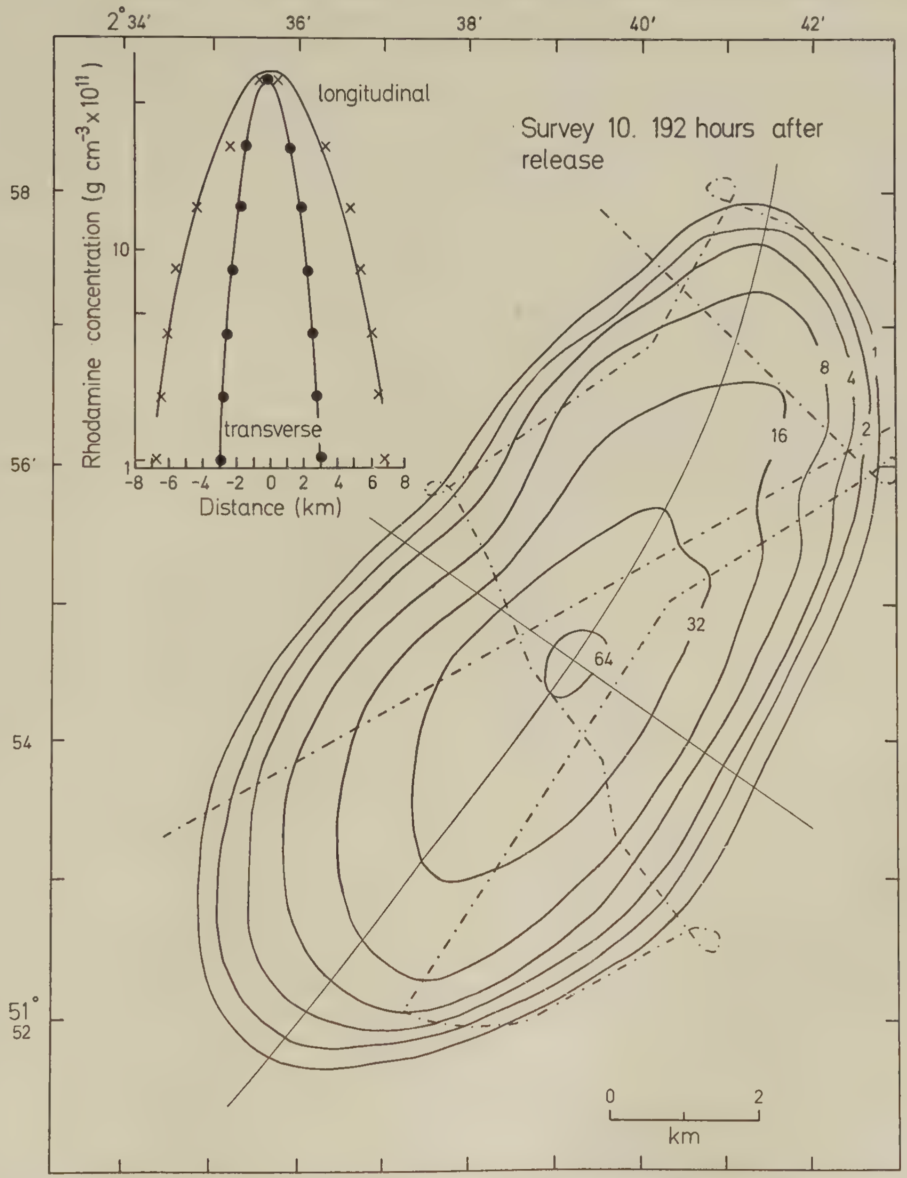


Figure 21. Distribution measured in January 1969 192 h after the release of Rhodamine-B. for further explanation see caption to Figure 16.

the advective terms. Since currents in the sea do not vary perfectly smoothly, as represented in Equation (10) the irregularities in the displacement inherent in this method are not altogether unreasonable when compared with typical conditions in the sea.

At the surface and bottom boundaries a complete reflection has been assumed so that there is no transport across the boundary. The vertical boundaries have been less well represented in the interests of economy in computer space. Some loss of material does take place at these boundaries but this is kept small by using an array that is large enough to give very low concentrations in the boundary area. As a check on the loss of material in this way the total mass of substance represented at each stage of the calculation is computed. A simplified flow chart of the programme is given in Figure 23.

It is clear that the numerical simulation of diffusion that has been adopted demands a fairly small horizontal grid spacing and a value of 50 m has been

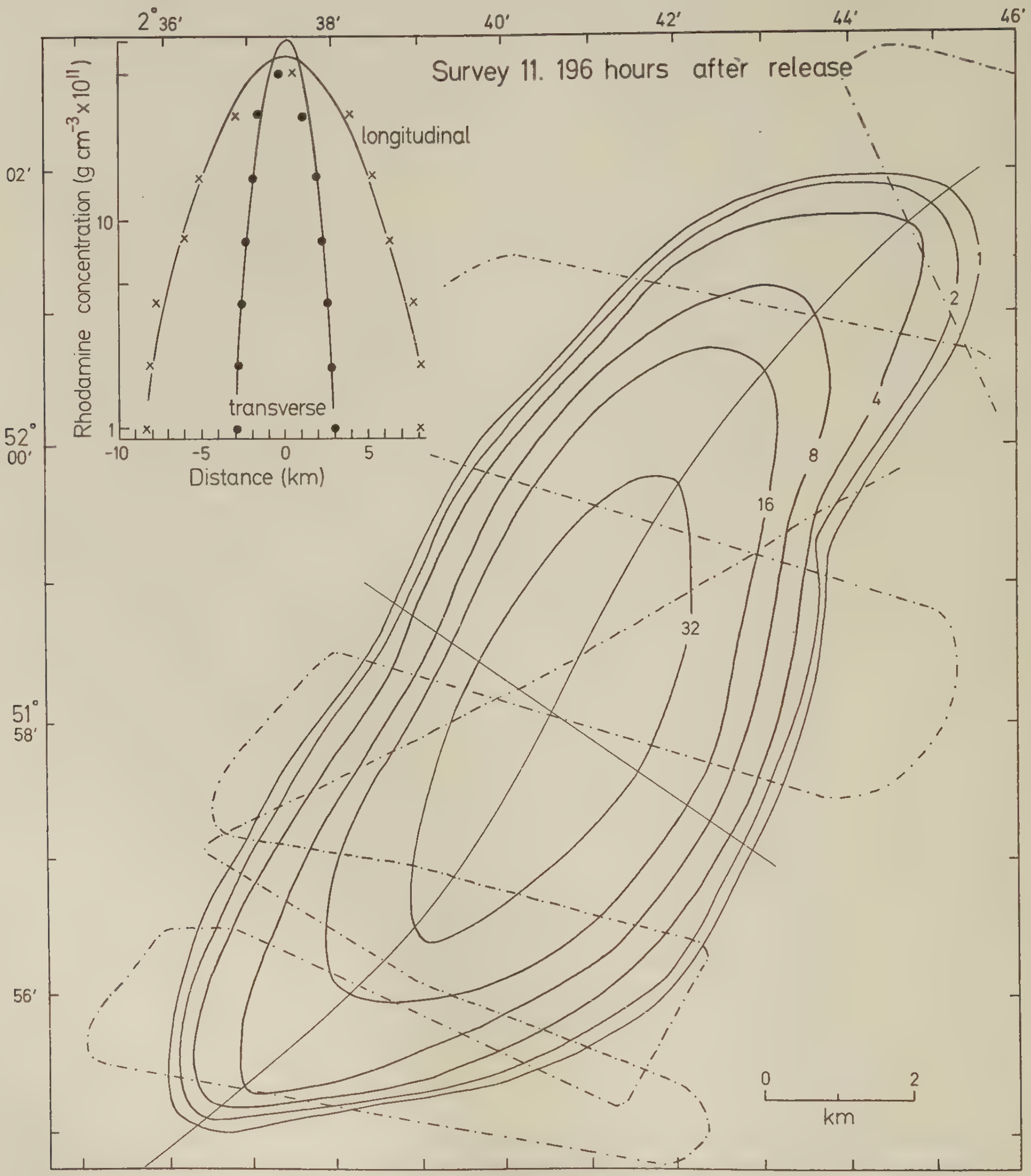

2°36'
38'
40'
42'
44'
46'
02'
52° 00'
51° 58'
56'
Survey 11. 196 hours after release
longitudinal
transverse
Rhodamine concentration (g cm^{-3} x10^{11})
10
1
-10
-5
0
5
Distance (km)
1
2
4
8
16
32
0
2
km

Figure 22. Distribution measured in January 1969 196 h after the release of Rhodamine-B. For further explanation see caption to Figure 16.

used in most trial runs of the programme. For comparison, a grid spacing of 25 m was also used but the results suggested that for runs over a few hours 50 m was small enough to provide an acceptable approximation.

The programme is now being applied to investigate the effect of using different values for the eddy diffusion coefficients, particularly the vertical coefficient, in order to reproduce the horizontal distributions measured in January 1969 and described above. A comparison of predicted and observed distributions shows clearly the major importance of the vertical shear diffusion process rather than horizontal eddy diffusion in this area. The horizontal eddy diffusion coefficients are therefore small although their precise value cannot be determined; a value of 1000 cm^2/s has been used. With a vertical diffusion coefficient of 100 cm^2/s a fair approximation to the distributions observed at the first four surveys is obtained (Figs 14 and 15). Results from the mathematical model therefore confirm earlier conclusions that in the Southern Bight the vertical shear process is more important than horizontal turbulence in producing horizontal dispersal. It seems that in this area the diffusion process is not strongly scale-dependent and the results of the Rhodamine-B and model investigations are thus consistent with the supposition made earlier that diffusion rates at the scale of the plaice egg distributions are comparatively low.

The influence of hydrographic factors on the movement and dispersal of the plaice egg distributions in 1962 and 1969

It was concluded above that development of the plaice egg and larval distributions in 1962 and 1969 showed notable differences which may have been related to a significant difference in some feature of the circulation in those 2 years.

Two aspects have been considered:

(1) the possible influence of large-scale circulation features and

(2) changes in the local circulation.

The influence of large-scale circulation

The European shelf seas experience periods of 3–4 years during which salinities tend to increase due to the influx of saline water from the eastern Atlantic (Dickson, 1971). Each period of rising salinity is followed by a shorter period in which salinity values fall. Dickson has commented that the salinity fluctuations are roughly contemporaneous events in all areas of the European shelf seas. His results show that at the time of the 1962 and 1969 plaice spawning seasons salinities in the Baltic were respectively at about minimum and maximum values. It is possible that the time of these spawnings relative to the Atlantic inflow cycle was influential in determining the development of the larval distributions. Within the Southern Bight the 14 day mean salinity at the North Hinder lightvessel rose slightly over the period 1 January to 1 April 1969, but fell appreciably over the corresponding period of 1962. However, these salinities could be influenced by other factors than inflow and no clear connection has been established between the Atlantic inflow cycle and the development of the plaice larval distributions.

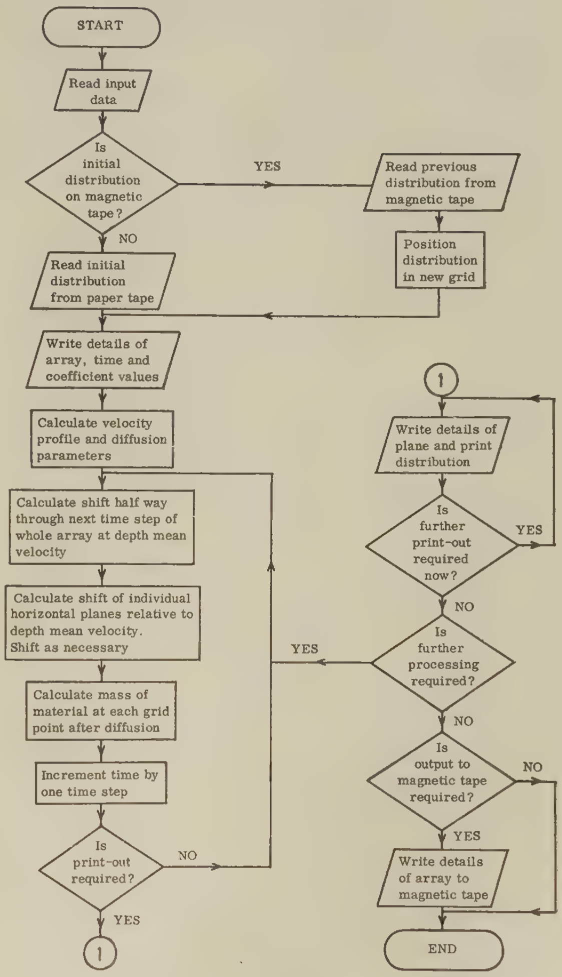

START
Read input data
Is initial distribution on magnetic tape?
YES
NO
Read previous distribution from magnetic tape
Position distribution in new grid
Read initial distribution from paper tape
Write details of array, time and coefficient values
Calculate velocity profile and diffusion parameters
Calculate shift half way through next time step of whole array at depth mean velocity
Calculate shift of individual horizontal planes relative to depth mean velocity. Shift as necessary
Calculate mass of material at each grid point after diffusion
Increment time by one time step
Is print-out required?
NO
YES
1
1
Write details of plane and print distribution
Is further print-out required now?
YES
NO
Is further processing required?
YES
NO
Is output to magnetic tape required?
NO
YES
Write details of array to magnetic tape
END

Figure 23. Simplified flow chart for numerical simulation of vertical shear diffusion.

Variation of the local circulation

Water movements in the Southern Bight must reflect changes in the circulation of the southern North Sea as a whole and also the discharge from the main estuaries feeding the area and especially that of the Rhine. One important local hydrographic feature is the inflow or loss of water through the Dover Strait, which must produce corresponding movement of the water in the Southern Bight, and Bowden (1956) has shown that regional winds exert a major influence on this flow. His results, which are consistent with those of Lawford and Veley (1955), showed that winds from a little west of south are the most effective in causing an inflow of water from the Channel to the North Sea, although Wyrtki (1952) had earlier suggested that the optimum wind direction

Table 9. Frequency of wind strength and direction at the North Hinder lightvessel over the period of the larval surveys in 1962 and 1969

February 1962

Wind force	N	NE	E	SE	S	SW	W	NW	C
0..........	–	–	–	–	–	–	–	–	1
1..........	1	–	–	–	–	1	1	2	–
2..........	–	2	–	–	–	–	9	1	–
3..........	2	2	1	–	–	9	6	5	–
4..........	4	3	2	–	–	7	6	7	–
5..........	10	4	–	–	2	6	5	7	–
6..........	5	22	13	–	2	6	2	3	–
7..........	5	11	6	–	–	3	6	3	–
8..........	5	–	–	–	–	1	5	6	–
9..........	4	–	–	–	–	2	1	4	–
10..........	1	–	–	–	–	–	–	2	–
Total.......	37	44	22	–	4	35	41	40	1

February 1969

Wind force	N	NE	E	SE	S	SW	W	NW	C
0..........	–	–	–	–	–	–	–	–	2
1..........	–	–	2	–	–	–	–	–	–
2..........	–	2	2	–	4	–	–	2	–
3..........	6	4	8	4	2	–	2	6	–
4..........	12	4	36	10	6	–	8	6	–
5..........	10	–	8	–	2	2	2	6	–
6..........	4	12	10	–	2	4	6	18	–
7..........	2	2	2	–	–	–	–	4	–
8..........	–	–	–	–	–	–	–	–	–
9..........	–	–	–	–	–	–	–	–	–
10..........	–	–	–	–	–	–	–	–	–
Total.......	34	24	68	14	16	6	18	42	2

Period covered by larval surveys,
26 January–28 March 1962

Wind force	N	NE	E	SE	S	SW	W	NW	C
0..........	–	–	–	–	–	–	–	–	3
1..........	5	7	1	4	3	1	3	3	–
2..........	9	8	8	3	5	1	12	7	–
3..........	22	24	15	6	1	12	13	12	–
4..........	15	27	7	6	1	11	18	20	–
5..........	15	14	–	–	2	12	6	9	–
6..........	5	24	14	2	3	10	2	3	–
7..........	5	11	8	2	–	4	6	3	–
8..........	5	–	–	–	–	1	5	6	–
9..........	4	–	–	–	–	2	1	4	–
10..........	1	–	–	–	–	–	–	2	–
Total.......	86	115	53	23	15	54	66	69	3

Period covered by larval surveys,
26 January–3 April 1969

Wind force	N	NE	E	SE	S	SW	W	NW	C
0..........	–	–	–	–	–	–	–	–	2
1..........	–	2	4	–	2	–	2	–	–
2..........	–	8	10	2	6	2	–	2	–
3..........	6	18	24	8	2	12	4	6	–
4..........	24	52	82	12	22	12	24	12	–
5..........	16	6	46	2	2	6	2	6	–
6..........	4	12	22	–	2	10	10	18	–
7..........	2	2	4	–	–	–	6	4	–
8..........	–	–	–	–	–	–	–	–	–
9..........	–	–	–	–	–	–	–	–	–
10..........	–	–	–	–	–	–	–	–	–
Total.......	52	100	192	24	36	42	48	48	2

is south-southeast. The strength and direction of surface winds at the North Hinder lightvessel over the period of the 1962 and 1969 investigations are given in Table 9; the information being based on Anon (1965) for the earlier period and on data provided by Professor R. Dorrestein of Koninklijk Nederlands Meteorologisch Instituut for 1969. The table shows that in 1969 winds from southwest or west were less frequent and less strong than in 1962 and that in 1969 there was a much greater proportion of winds from the east, but strong northeast winds occurred more frequently in 1962. However this data provides no clear prediction that inflow from the Channel will have been generally at a lower level in 1962 than in 1969.

Variation of the surface salinity distribution has also been considered. In 1962 surveys of the surface salinity were made by RV "Clione" over the periods 4–10 January and 24 March–1 April (Fig. 24). A survey of the surface salinity was also made by RV "Ernest Holt" over the period 4–23 January 196 and distributions for the period 17–28 February an 24–29 March were reported by Tijssen (1969) an Otto et al (1969) (Fig. 25). The intervals betwee these surveys cover an important part of the perio spanned by the plaice egg surveys. The results sho that from January to March 1962 the area in th Southern Bight within the 34·5‰ isohaline de

Table 10. Mean monthly flow in m³/s of the Rive Rhine, measured at Lobith

Year	Dec	Jan	Feb	Mar
1961	2 904	–	–	–
1962	–	2 910	3 779	2 291
1968	1 606	–	–	–
1969	–	2 058	2 403	3 324

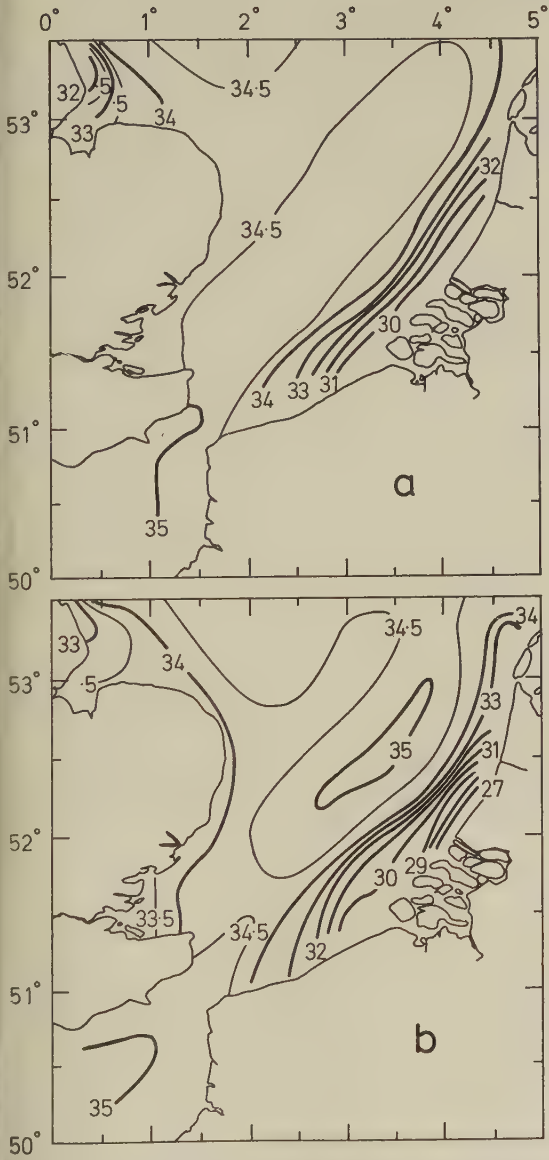
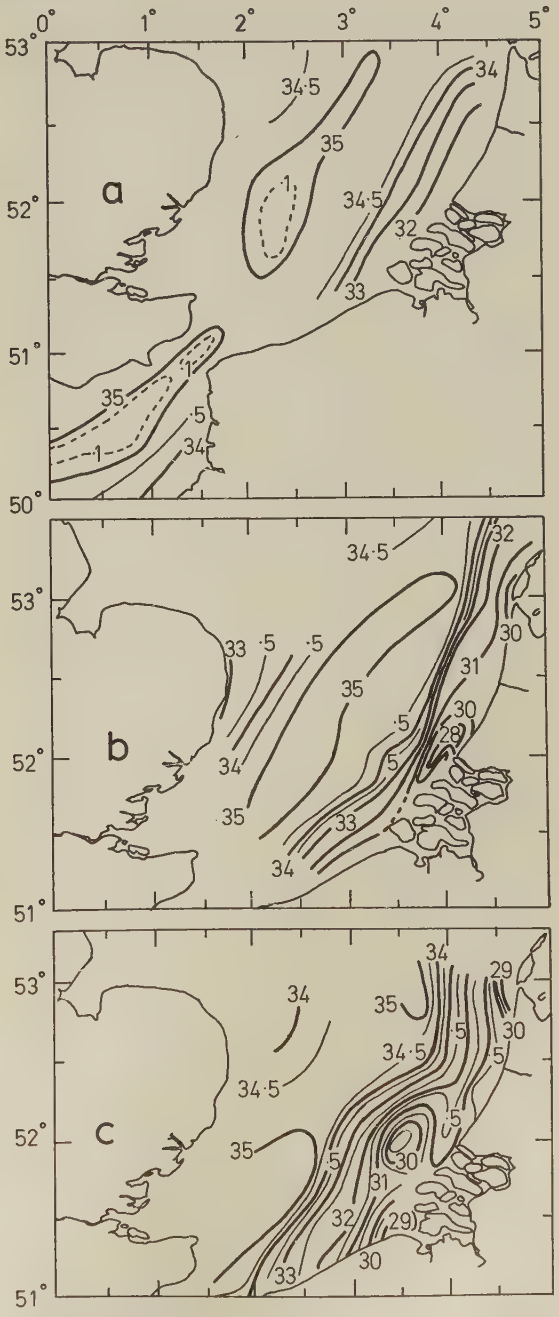

0°
1°
2°
3°
4°
5°
53°
52°
51°
50°
32
·5
·5
33
34
34·5
34·5
32
30
34
33
31
35
a
33
·5
34
34·5
34
33
35
31
27
29
30
33·5
34·5
32
35
b

Figure 24. Surface salinity distribution (‰) in the Southern Bight at times during the 1962 plaice egg surveys; (a) 4–10 January and (b) 24 March–1 April.


0°
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34
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33
·5
·5
30
31
35
30
·5
28
b
34
·5
35
33
34
34
29
34
35
30
·5
34·5
·5
34·5
·5
c
35
·5
30
31
32
29
30
33

Figure 25. Surface salinity distributions (‰) in the Southern Bight at times during the 1969 plaice egg surveys; (a) 4–23 January, (b) 17–28 February and (c) 24–29 March.

creased somewhat, but at the later survey there was a small area with a salinity greater than 35‰. The presence of the latter suggests that some high-salinity water entered the Southern Bight from the Channel towards the end of the period between the surveys, but it appears that over this period as a whole inflow was at a generally low rate. The 1969 distributions show no remarkable changes in salinity but by the end of March there was clearly a large volume of low salinity water off the mouth of the Rhine and extending a considerable distance offshore. The records of Rhine flow (Table 10) show that in 1962 the outflow in March was some 20% less than the previous December and January, whereas from December 1968 to March 1969 the outflow increased steadily, the March flow being double that in December. This increased run-off from the land, which may have occurred on both sides of the Southern Bight, could have masked any tendency for the salinity to increase in 1969 due to inflow from the English Channel. Alternatively, it is possible that evaporation may have played a part in determining the salinity since Vaux (1953) has pointed out that this may be of significant importance, particularly during periods of east to northeast winds. However, as has already been seen, it is not apparent from the wind records that easterly winds will have been more important in 1962 than in 1969. Thus none of the hydrographic features so far considered leads to a satisfactory explanation for the differences in plaice larval dispersal noted between the two years 1962 and 1969.

A further hydrographic feature is the inflow of water through the Dover Strait and one of the best estimates of this for the periods in question results from using the voltage induced across the St Margaret's Bay-Sangatte telephone cable (Bowden, 1956; Cartwright, 1961). Unfortunately the recording arrangements at Dover were found to be faulty in 1965 and were changed. It was therefore necessary to check that the calibration applicable in 1962 was still valid in 1969. Cartwright (1961) gave the calibration factor for the cable as $58{\cdot}3 \times 10^6$ ft^3/s/V or $1{\cdot}65 \times 10^6$ m^3/s/V and found that there was a back e.m.f. which he estimated as 0·083 volt. Harmonic analysis of part of the 1969 record and comparison with the predicted value of the M_2 component has shown a calibration factor close to that given earlier by Cartwright. Thus, although it has not yet been possible to check the back e.m.f. it seems that the best available expression for flow through the Dover Strait in terms of cable voltage V is $1{\cdot}65 \times 10^6 (V + 0{\cdot}083)$ m^3/s, where V is taken as positive for a flow to the northeast.

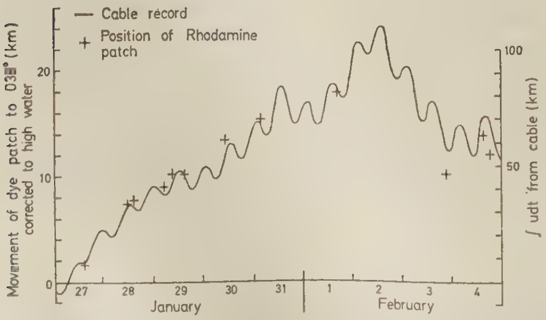

Figure 26. Observed movement of Rhodamine-B patch compared with displacement calculated from telephone cable data. For further explanation see text.

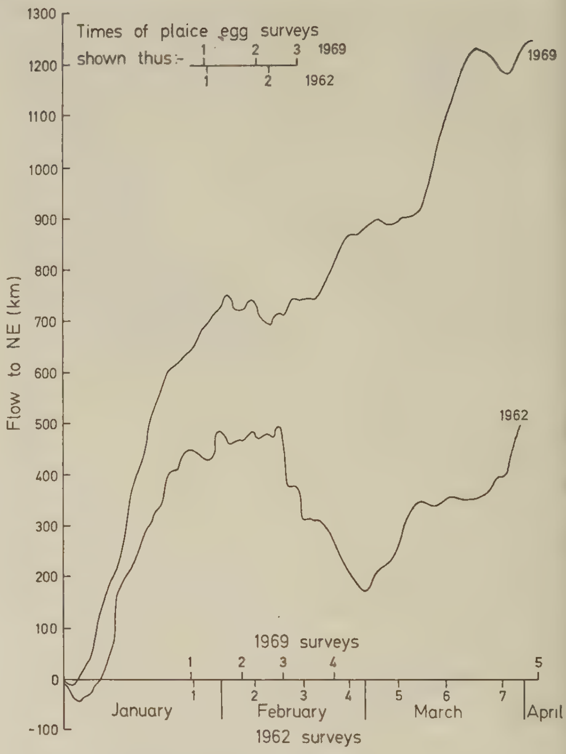

Figure 27. Displacement of water through the Dover Strait for the periods of the 1962 and 1969 plaice egg surveys, based on telephone cable data.

Dr Cartwright has kindly provided data of the cable voltage variation for the periods of the 1962 and 1969 surveys. In the case of the latter period it is possible to compare the flow through the Dover Strait with the current meter data and also with the observed movement of the Rhodamine-B patch. The 25-hour residuals calculated from the cable record are compared with the current meter data in Figure 11. The two show a marked interpendence but residual flows calculated from the cable appear to be about 4·5 times greater than those given by the current meters. Since the flows are given as velocities this result is not surprising when the cross section of the transect at Dover is compared with that in the central Southern Bight. The cable record has also been compared with the observed movement of the Rhodamine-B patch. In this case the displacement of the dye patch has been compared with the displacement calculated from the cable record (Fig. 26). Again, when allowance is made for a factor of about 4·5 between flow at Dover and that in the central Southern Bight, good agreement is obtained. This suggests that the cable records may usefully be applied to the determination of the water drift in the Southern Bight over the whole period of the 1962 and 1969 surveys, for the greater part of which no current meter data are available, and Figure 27 shows the displacements calculated for these two periods. From early January until mid-February the flow through the Strait was similar in the 2 years. The main difference was in the second half of February; in 1962 over this sub-period there was an appreciable loss of water to the English Channel, much of which was in fact associated with northwesterly gales in the North Sea on 14 and 17 February. In contrast over the corresponding period of 1969 water was entering the Southern Bight from the Channel and in mid-March a particularly marked inflow occurred over a period of more than one week. The greater inflow shown by the cable for 1969 is consistent with Dickson's (1971) ideas on long-term variations of the Atlantic inflow. The main source of error in interpreting the cable voltage data is probably the cable back voltage which is often of the same order as the component of the signal corresponding to steady drift. Examination of the 1969 results suggests that this back voltage correction may have been rather smaller than allowed for in the expression used. However the difference in the residual flow in late February in the 2 years appears to be well established and it seems that this represents the main difference in the hydrographic conditions in these 2 years and was a major cause of the different dispersal of plaice larvae observed and commented upon above.

Summary

Examination of the distribution of plaice eggs and larvae in the Southern Bight of the North Sea for the years 1962, 1963 and 1969 has shown that considerable variation in the spread of the distributions can occur from year to year. In 1963 distributions were much less widespread than in the other 2 years. However, as individual distributions develop through egg and larval stages, there is remarkably little evidence of spreading out from survey to survey even when the work covers total periods of up to 60 days. This observation suggests that turbulent diffusion in this sea area is a comparatively slow process. The results of the tracer experiment support this suggestion and indicate that the main process of diffusion in this area results from the interaction of vertical tidal shear and vertical mixing due to turbulence. This hypothesis is further supported by a mathematical simulation of diffusion which shows that the observed rates of diffusion are consistent with reasonable values of the vertical diffusion coefficient taken in conjunction with values of the vertical velocity shear deduced from current meter observations. In contrast with diffusion produced by horizontal turbulence the vertical shear process does not produce faster rates of diffusion for larger distributions and the plaice egg distributions are relatively large. Overall therefore these results lead to the conclusion that in this area horizontal turbulence has little effect on dispersion, which is mainly produced by the vertical shear process.

Although there appears to be very little dispersal of distributions due to diffusion, the water circulation in the Southern Bight is important in determining the general movement of the egg and larval distributions and also in affecting the shape of them, considerable differences being found between the results for 1962 and 1969. Current meter results from an area some 36 km square in the central Southern Bight show that residual drift in the direction of the main tidal axis varies very little from place to place within this area. This drift shows a good correlation with the southwesterly component of the wind but this is thought to be due to the general influence of surface winds on the circulation in a larger area including the Dover Strait rather than the result of a local wind-water interaction. Residual drift in the central Southern Bight as shown by the current meters along the main tidal axis and as shown by the Rhodamine patch is proportional to flow through the Dover Strait, but in the latter area the amplitude is 4·5 times greater. The notable movement of the egg and larval patches towards the northeast in 1969 corresponds to a stronger inflow from the English Channel during the same period.

Acknowledgements

In the course of the work described above I have been indebted to numerous colleagues both at the Fisheries Laboratory and elsewhere. In particular I would mention Mr D. Harding of this laboratory who has made available to me the basic data of egg and larval distributions without which the work would have been impossible. For providing the North Hinder wind data I am indebted to Professor R. Dorrestein of KNMI and for information of the Rhine flow to Dr K. P. Blumenthal of Rijkswaterstaat. It is also a pleasure to thank Dr D. W. Cartwright of IOS, Bidston who gave me Dover telephone cable data and who patiently answered my questions about calibration of the cable e.m.f. Finally I gratefully acknowledge the help of those who were with me throughout the work, Mrs M. J. Boon, Mr J. Wooltorton and my wife.

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Sources of errors in and limitations of Virtual Population Analysis (Cohort Analysis)

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Various sources of errors in Virtual Population Analysis (VPA) are discussed. Errors in the assumed value of natural mortality create errors in estimated fishing mortalities of about the same size but with opposite sign if the total mortality varies moderately from year to year and the true natural mortality is constant. Stock size will be over- or under-estimated when natural mortility is over- or under-estimated, but estimated relative changes in stock size from year to year will be approximately correct. Fluctuations in total mortality caused by random fluctuations in natural mortality from year to year will disappear almost completely in VPA if a constant natural mortality is assumed. A trend in the true natural mortality with time or age will be converted to a trend in the VPA estimates of fishing mortalities. Relative strength of weak and strong year classes will be wrongly estimated by VPA if the true natural mortality varies with year class strength, and this may influence various regression lines commonly used for predicting year class strength from young fish survey indices. Errors in VPA caused by uneven distribution of natural or fishing mortality throughout the year are shown to be generally small and negligible. Effects of stock migration on VPA are discussed. For a year class which continuously migrates from an area A to an area B at a constant emigration rate, equations which give the number of fish of the year class at any time in each of the two areas are developed. These equations may be utilized in a technique similar to VPA for retrospective analysis, and the application of this technique is illustrated. If emigration is included in the natural mortality the traditional VPA may successfully be used in area A. There is, however, no simple way to adjust for immigration in area B, and the traditional VPA may give a completely wrong picture of the situation in this area.

1. Introduction

The Virtual Population Analysis or Cohort Analysis is extensively used in stock assessment both within ICES and other scientific bodies. It is an extremely useful technique for estimating past values of fishing mortalities and stock sizes. These past values may be utilized to get indications of the present state of the stock and the prospects for the coming years. Because of the extensive use of the method it is however, important to know the limitations of it and the various sources of errors. Contributions on this were given by Pope (1972) and Agger, Boëtius and Lassen (1971). In this paper some further aspects will be discussed.

2. Clarifications of terms used

The term Virtual Population was introduced by Fry (1949) and defined as the sum of the catches of a year class which has passed through the fishery. Gulland (1965) developed a way of estimating population and fishing mortality by a stepwise correction of the virtual population. Identical results can be obtained without involving the virtual population at all. Given the two equations for catch of a year class in year i and stock size in year i and $i+1$

$$C_i = N_i[F_i/(F_i + M)]\{1 - \exp[-(F_i + M)]\}$$
$$N_{i+1} = N_i \exp[-(F_i + M)]$$

where

C = catch in number
N = stock size in number
F = instantaneous fishing mortality
M = instantaneous natural mortality

F_i and N_i may be found either by iteration or by reference to tables if N_{i+1}, C_i and M are known. Having estimated F_i and N_i, one can then go back to year $i-1$ and so on. For the last year (the starting year for the analysis) one has to assume a value for N or calculate N from an assumed or estimated value of F.

It is this method which at present is called Virtual Population Analysis (VPA). It is essentially nothing more than using the Beverton and Holt (1957) equations backwards instead of forwards, and it makes no use of Fry's Virtual Population. The solution of the equations was discussed by Murphy (1965). Unfortunately it has caused some confusion that the method now is called Virtual Population Analysis. The term Cohort Analysis was used by Pope (1972) for a method similar to VPA, the only difference being that the approximate formula

$$N_i = C_i \exp(M/2) + N_{i+1} \exp(M)$$

is used instead of solving the two simultaneous equations given above.

3. Effects of wrong starting value for $N(F)$ and sampling errors of the catch data

These aspects were discussed by Pope (1972) and will not be further discussed in any detail in this paper. Pope showed that such errors converge to fairly small values as one calculates the strength of a class backwards. It should be stressed that the relative error in $N(F)$ in year i when starting with a wrong value of $N(F)$ in year t is not determined by the size of the time period between year i and year t but by the cumulative fishing mortality during the period. The estimates converge rapidly towards the true values when the fishing mortality is high. With low fishing mortalities the convergence is slower and in the extreme case when F/M approaches O there will be almost no convergence as one calculate backwards year for year.

4. Effects of errors in the natural mortality (M)

(i). Constant natural mortality

One common way of estimating the starting value of fishing mortality is to estimate total mortality Z_t from catch per unit of effort data and then calculate F_t by $\hat{F}_t = \hat{Z}_t - \hat{M}$.[1] The estimate of Z will be independent of any assumption about natural mortality. It will therefore be assumed here that the final $\hat{Z}_t$ is correct.

Then $\hat{F}_t = \hat{Z}_t - \hat{M}$ will be in the same absolute error as M, but with opposite sign for the error ($\hat{F}_t - F_t = M - \hat{M}$).

From the equation

$$C_t = N_t(F_t/Z_t)[1 - \exp(-Z_t)]$$

it follows that

$$\frac{N_t F_t}{Z_t}[1 - \exp(-Z_t)] = \frac{\hat{N}_t \hat{F}_t}{Z_t}[1 - \exp(-Z_t)]$$

(*C* is given)

i.e.

$$N_t F_t = \hat{N}_t \hat{F}_t$$

$$\frac{\hat{N}_t}{N_t} = \frac{F_t}{\hat{F}_t} = \frac{Z_t - M}{Z_t - \hat{M}}$$

If Z is constant from year to year, the last equation will be valid for all years when one calculate the stock backwards by VPA. $Z_i (i < t)$ and the relative changes in stock size from year to year will be correctly estimated by VPA, but stock size will be over- or underestimated when M is over- or underestimated, and the relative error is given by the equation above. The error in $\hat{F}$ will be constant and equal to $M - \hat{M}$.

If Z varies from year to year errors in $\hat{M}$ also generally will give errors in $\hat{Z}_i$ and therefore errors in estimated relative changes in stock size. However, the errors in $\hat{Z}_i$ will be fairly small if the fluctuations in Z_i are moderate. This may be illustrated by the following example.

Assume F_i fluctuates randomly from year to year on a year class as shown in Figure 1, where F_i varies between 0·42 and 0·83, and assume $M = 0{\cdot}2$. The

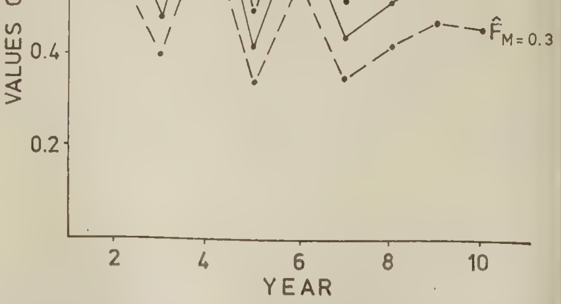

Figure 1. Estimated F-values assuming $M = 0{\cdot}1$ and $M = 0{\cdot}3$ in VPA plotted together with true F-values ($M = 0{\cdot}2$).

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[1] A caret mark above a symbol denotes an estimated or assumed value.

two dotted lines in Figure 1 show estimated F-values from VPA assuming $M = 0\cdot1$ and $M = 0\cdot3$, using the catches corresponding to $M = 0\cdot2$ and the true total mortality for the last year when estimating starting values for N_t in the VPA. The true and estimated total mortalities are plotted in Figure 2.

As expected $M = 0\cdot1$ gives too high $\hat{F}$-values and $M = 0\cdot3$ gives too low $\hat{F}$-values. The differences between estimated and true Z-values are small, the biggest differences (about 0·04) occur when the change in $Z(F)$ from one year to another is large. For both $M = 0\cdot1$ and $M = 0\cdot3$ the estimated Z-values fluctuate around a mean value approximately equal to the true mean. A low $M(0\cdot1)$ tends to overestimate fluctuations in Z and thereby overestimate F to a smaller extent when F is low than when F is high, while a high $M(0\cdot3)$ tends to underestimate fluctuations in $Z(F)$ and thereby underestimate F to a smaller extent when F is low than when F is high. This has one important consequence: if the estimated F-values using wrong M are plotted against fishing effort, the wrong M will not generally cause a significant intercept of the regression line on the F-axis which then could indicate that a wrong M was used. This is illustrated in Figure 3 where true F-values (effort) are plotted against estimated F-values using $M = 0\cdot1$ instead of the correct $M = 0\cdot2$. (In order to get a wide range of F-values the deviations of the individual true F's from their mean were made twice as big as in Figure 1. The $\hat{F}$-values corresponding to $M = 0\cdot1$ were then estimated by the method used for Fig. 1 – Fig. 2). The estimated regression line has an intercept on the F-axis of only 0·022 while the error in M is $-0\cdot1$.

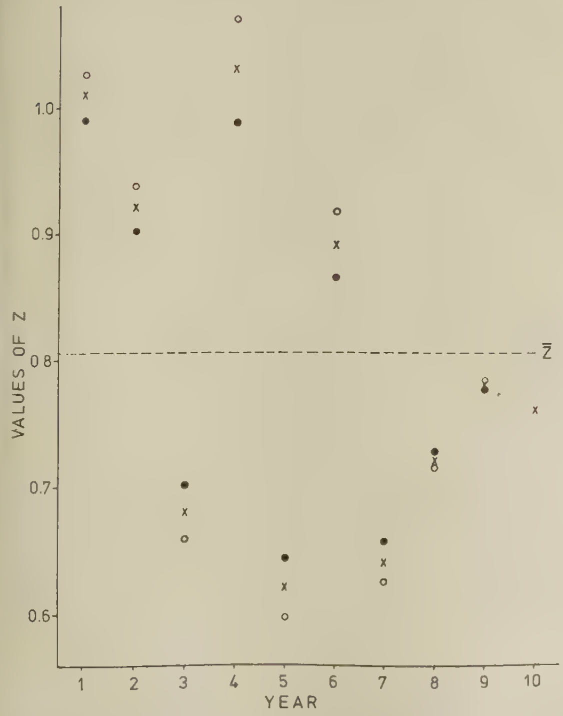

Figure 2. Estimated Z-values assuming $M = 0\cdot1$ and $M = 0\cdot3$ plotted together with true Z-values ($M = 0\cdot2$). Key to symbols: ●, $Z_{M=0\cdot3}$; ○, $Z_{M=0\cdot1}$; ×, Z.

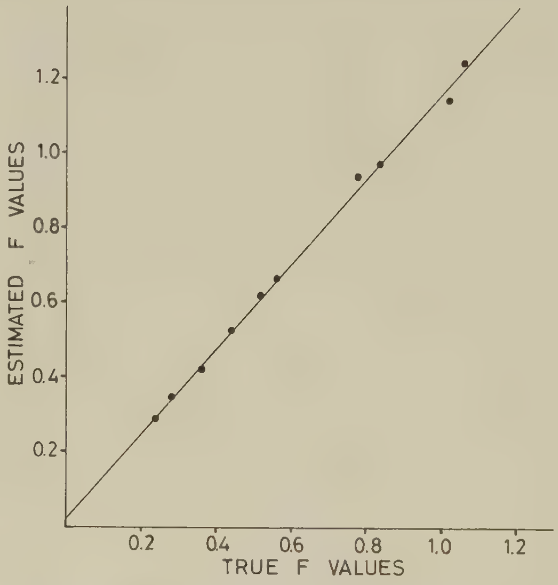

Figure 3. Regression of estimated F-values from VPA assuming $M = 0\cdot1$ against true F-values ($M = 0\cdot2$).

(ii). Natural mortality varies

If M varies randomly from year to year, this will cause a component of random fluctuations in the total mortality Z. These fluctuations will disappear almost completely in the VPA estimates if a constant natural mortality $\hat{M}$ is assumed. Disregarding errors caused by wrong starting values in the VPA, the estimated F-values ($\hat{F}$) generally will follow the same trend as the true F's. The level may be different depending on the relation between $\hat{M}$ and the mean value $\bar{M}$ around which the true natural mortality fluctuates.

The effects of random fluctuations in M are illustrated in Figure 4. M varies around a mean value of 0·2 with lowest and highest value being 0·12 and 0·30 respectively (Fig. 4a). Assuming a constant fishing mortality of 0·2, the total mortality Z fluctuates to the same extent as $M(Z = M + 0\cdot2)$. When a constant $M = 0\cdot2$ was assumed in a VPA (using catches corresponding to true M and F, and assuming $\hat{Z} = Z$ for the last year), the estimated F-values

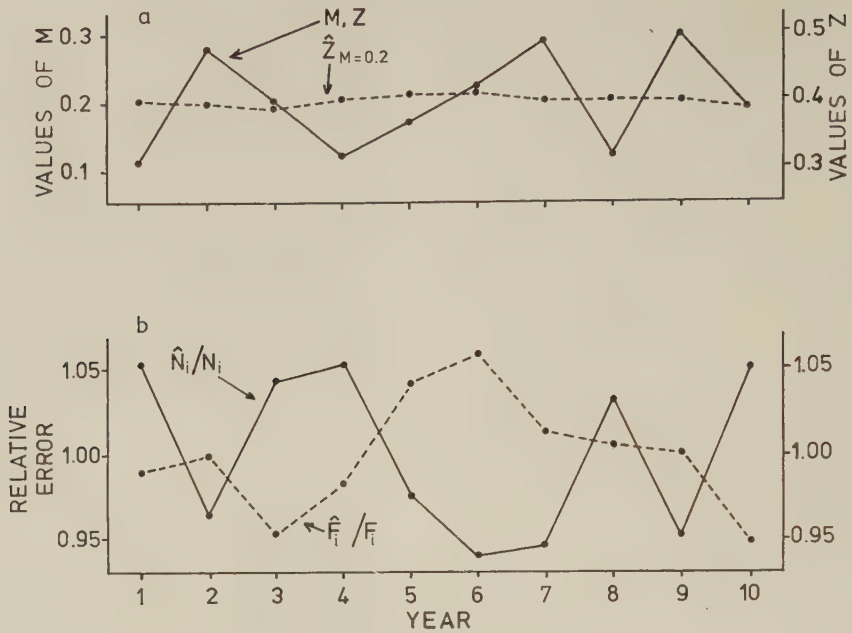

Figure 4. (a) Estimated total mortality ($\hat{Z}$) plotted together with true (varying) natural and total mortality and (b) relative errors in $\hat{N}_i$ and $\hat{F}_i$. M assumed equal to 0·2 in VPA. $F = 0{\cdot}2$.

were nearly constant with a maximum value of 0·212 and a minimum value of 0·19. Thus, the highest relative error in $\hat{F}$ was only about 6% (Fig. 4b), but the fluctuations in Z almost completely disappeared (Fig. 4a). The highest relative error in stock size estimates ($\hat{N}_i$) was also only about 6% (Fig. 4b).

In conclusion, errors in $\hat{F}_i$ and $\hat{N}_i$ from VPA caused by random fluctuations in M are likely to be small when M fluctuates moderately. The largest errors will appear in the estimated total mortalities $\hat{Z}_i$.

A trend in M with time or age will cause trends in the errors in $\hat{N}_i$, $\hat{F}_i$ and $\hat{Z}_i$ with time or age if a constant M is assumed in a VPA.

For illustration an example was constructed where M varied with age (i) of a year class according to the equation

$$M_{i+1} = M_i[1 - (M_i - 0{\cdot}1)], \quad M_1 = 0{\cdot}3 \quad \text{(Fig. 5a)}$$

M approaches the asymptotic value 0·1 as i increases (for very high i's a more realistic assumption would probably be that M started to increase again).

True values of N_i, F_i and Z_i were compared with estimated values from VPA (using catches corresponding to true values, and assuming $\hat{Z} = Z$ for the oldest age) for two constant F-values $F = 0{\cdot}2$ and $F = 0{\cdot}6$. Two different constant M's, $M = 0{\cdot}1$ and $M = 0{\cdot}2$, were used in VPA, and this resulted in four VPA's two for $F = 0{\cdot}2$ (Fig. 5b) and two for $F = 0{\cdot}6$ (Fig. 5c).

Generally, the errors in $\hat{N}_i$ and $\hat{Z}_i$, and the relative errors in $\hat{F}_i$, decreased when F increased from 0·2 to 0·6. As F increases a larger portion of the total mortality is comprised by F and therefore the errors created by wrong M-values in the VPA's decrease.

For both F-values $\hat{Z}$ underestimated Z and the errors in $\hat{Z}$ increased as i (age) decreased both for $M = 0{\cdot}1$ and $M = 0{\cdot}2$. That this was the case also for $M = 0{\cdot}2$ (which is in between the range of the true M-values and almost equal to the true M for age 3) illustrates the fact that it is not the differences $\hat{M}_i - M_i$ themselves which mainly cause the errors in $\hat{Z}_i$, but the changes with age in these differences created by changes in M_i (or Z_i cf. section 4(i)).

The $\hat{Z}_i$-values were a little smaller and $\hat{Z}_i - Z_i$ a little larger for $M = 0{\cdot}2$ than for $M = 0{\cdot}1$ (for $F = 0{\cdot}6$ the differences were insignificant). $M = 0{\cdot}2$ thus created the largest errors in $\hat{Z}_i$ even if $M = 0{\cdot}2$ is in between the actual range of the true M_i's while $M = 0{\cdot}1$ is outside this range. This illustrates the point mentioned in section 4(i) that changes in $\hat{Z}_i$ from year to year decreases when $\hat{M}$ increases. As Z_i continuously increases with decreasing age, a high constant $\hat{M}$ gives in this case larger errors in $\hat{Z}_i$ than

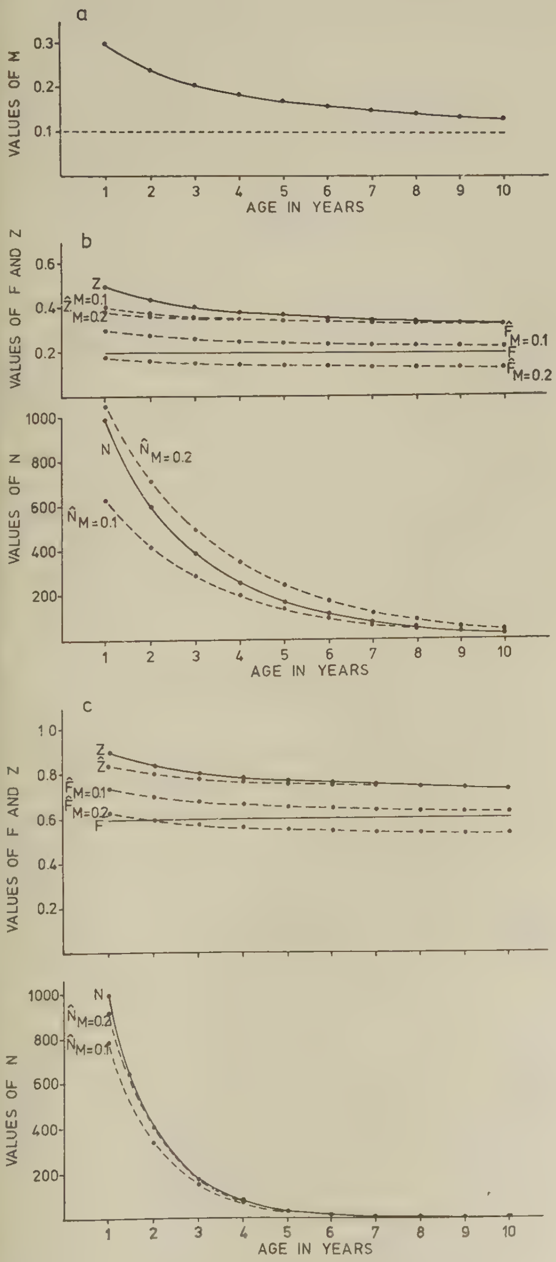

Figure 5. (a) Natural mortality plotted against age (i) when $M_{i+1} = M_i[1-(M_i-0{\cdot}1)]$, $M_1 = 0{\cdot}3$. (b) and (c): Estimated Z-values and F-values (upper figure) and N-values (lower figure) from VPA assuming $M = 0{\cdot}1$ and $M = 0{\cdot}2$ plotted together with true values when M varies with age as in (a). $F = 0{\cdot}2$ in (b) and $F = 0{\cdot}6$ in (c).

a low one, even if the higher M is nearer the true M_i's. In fact trials with other constant M's showed that $M = 0$ gave the best fit as far as Z_i was concerned.

For both F-values the estimated $\hat{F}_i$ (Fig. 5b–5c) increased with decreasing i. Thus, increasing natural mortality showed up as increasing fishing mortality in VPA. As expected for the older ages $M = 0{\cdot}1$ gave the smallest errors in $\hat{F}_i$, while $M = 0{\cdot}2$ gave the best fit for the youngest ages. The same was the case for N_i (Fig. 5b–5c). $M = 0{\cdot}1$ strongly underestimated N_1 for both F-values, while $M = 0{\cdot}2$ slightly overestimated N_1 when $F = 0{\cdot}2$ and slightly underestimated N_1 when $F = 0{\cdot}6$ ($F = 0{\cdot}6$ implies that a larger portion of the catch is taken when the year class is 1–3 years old and has a natural mortality even higher than the value 0·2, see Fig. 5a).

The strong underestimation of N_1 when the low $M = 0{\cdot}1$ was assumed has one interesting consequence: if in a certain stock the natural mortality is at a rather low and constant level for "normal" year classes but is higher at young ages for especially strong year classes, the VPA technique using a constant M will underestimate the strength of strong year classes at young ages relative to weaker year classes. For several stocks [e.g. North Sea Herring (Anon, 1975)] it has been observed that when the regression of VPA-strength of a year class against abundance indices from young fish trawl surveys is calculated, one gets a significant positive intercept on the VPA-axis. This may of course be a result of bias in the abundance indices from trawl surveys. From what is said above it follows, however, that this intercept also may be explained by a bias in the VPA results. This is illustrated in Figure 6. It is there

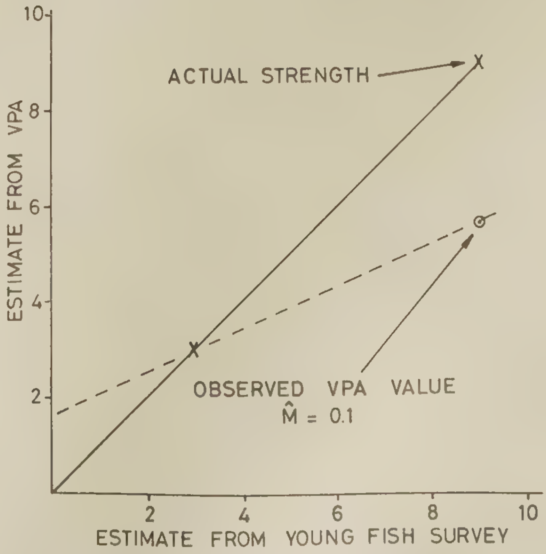

Figure 6. Relation between estimated strength of a year class from VPA and young fish trawl surveys when M varies with year class strength. For further explanation see text.

assumed that abundance indices from young fish surveys give unbiased relative strength of a year class at age 1. If a "normal" year class has a constant natural mortality of 0·1, but a year class three times stronger at age 1 has a natural mortality given by Figure 5a, a plot of VPA strength assuming $M = 0{\cdot}1$ against the young fish survey indices would give the dotted line in Figure 6, which has a large intercept at the VPA axis. (It is assumed that both year classes were fished at an $F = 0{\cdot}2$ from age 1 onwards).

5. Effects of seasonal variations in *F* and *M*

The Beverton and Holt catch equation

$$C_t = (N_tF_t/Z_t)[1 - \exp(-Z_t)]$$

is based on evenly distributed fishing and natural mortality throughout the year. If this is not the case, one will make errors both in a prognosis calculating the stock size N_{i+1} corresponding to given N_i and C_i and in a VPA calculating N_i corresponding to given N_{i+1} and C_i. The errors when calculating forwards (prognosis) and backwards (VPA) will, however, cancel out in the sense that when starting with the wrong $\hat{N}_{i+1}$ from the prognosis in the VPA, you will get back to the "true" N_i.

The size of the errors involved in a VPA when fishing mortality is not evenly distributed throughout the year is shown in Figure 7. It is there assumed that all catch is taken in the first or last quarter of the year. The relative errors in $\hat{N}_{i-1}$ starting with correct N_i are plotted against annual F (correct value taking into account the seasonal distribution of the catch) for different values of the natural mortality.

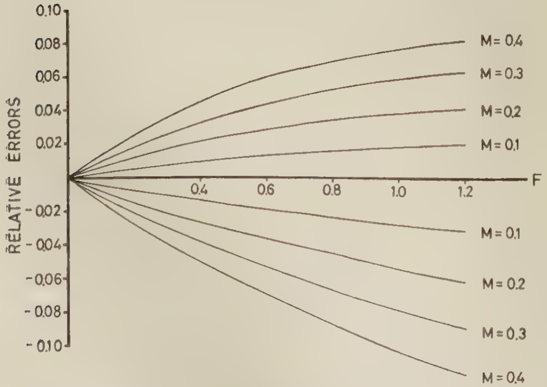

Figure 7. Relative errors in estimated $\hat{N}_{i-1}$ from VPA, caused by uneven seasonal distribution of the fishery, plotted against true annual fishing mortality. $\hat{N}_i$ is assumed to be equal to the true N_i. Positive errors: all catch is taken in the first quarter of the year. Negative errors: all catch is taken in the last quarter of the year.

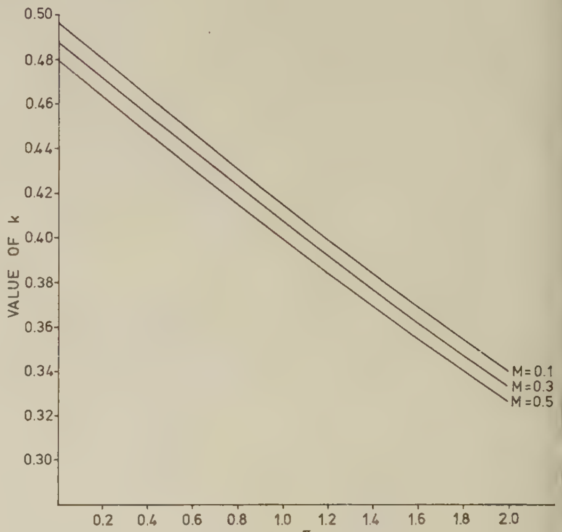

Figure 8. k in the relationship $N_i = C_i e^{kM} + N_{i+1} e^{M}$ plotted against F_i for $M = 0{\cdot}1$, 0·3 and 0·5.

The errors are generally small and negligible. One can get rid of these errors by carrying out the VPA on smaller time units than a year (if it is possible to give the catch on smaller time units). If this is done one should, however, also carry out any prognosis on these smaller time units, otherwise the errors in the prognosis may even increase because of the above mentioned "cancel out" nature of the errors.

In Pope's (1972) approximate formula

$$N_i = C_i \exp(M/2) + N_{i+1} \exp(M)$$

it is implicitly assumed that fish of a certain year class caught during year i have a mean life time of half a year in year i. If F and M are evenly distributed over the year this mean life time will, however, be less than half a year because there is a steadily decreasing number of fish in the sea, and therefore a steadily decreasing number of fish in the catch, during the year. The mean life time will decrease with increasing F and M.

The true relation between N_i and N_{i+1} may be written as

$$N_i = C_i \exp(kM) + N_{i+1} \exp(M)$$

where k is a function of F and M and may be interpreted as the mean life time. In Figure 8 k is plotted against F for various values of M. Instead of using Pope's approximate formula in the Cohort Analysis one may use the equation given above, assuming a value of k which corresponds approximately to the actual levels of F and M (if F does not vary too much from year to year).

If the fishery is typically seasonal it may be better to use the equation given above instead of the Beverton and Holt equations. One may then either define the beginning of the year as the main fishing season and put $k = 0$, or define the beginning of the year as 1 January and put k equal to the time period between 1 January and the main fishing season.

If fishing and natural mortality are evenly distributed over the year, a VPA on a monthly or quarterly basis will give exactly the same results as a VPA on an annual basis (if one starts with the same input stock size for the last year). The errors in $\hat{F}_i$ and $\hat{N}_i$ when calculating a year class backwards by VPA, caused by wrong starting values, will not decrease more rapidly when the number of time intervals are increased by using a smaller time unit. It is the cumulative fishing mortality, not the number of time units, which determines the rate of convergence towards the true values.

6. Stock migration

One of the largest sources of errors in the VPA technique lies in the implicit assumption made when carrying out a VPA on a stock area A that a fish caught in this area at age x also was in the area at any age $y < x$.

If a year class from a certain age on continuously migrates from an area A to an area B at a constant instantaneous emigration rate E, a VPA for area A will give correct values for N_i and F_i if E is included in the natural mortality for area A, i.e.

$$M'_{\mathrm{A}} = M_{\mathrm{A}} + E$$

where M_{A} is the "true" natural mortality and M'_{A} is the "apparant" natural mortality used in the VPA.

For area B, however, the situation will be much more complicated as far as the VPA is concerned. The number of fish of a certain year class which immigrates to the area at any time is determined by the number of fish left of the year class in area A, i.e.

$$dN_{\mathrm{AB}} = EN_{\mathrm{A}}dt$$

where N_{AB} is the number of fish which migrates into area B from area A. Therefore, one cannot adjust the VPA for area B simply by making an adjustment of the natural mortality as it could be done for area A.

Let

F_{A} = instantaneous fishing mortality in area A.
F_{B} = instantaneous fishing mortality in area B.
N_{A} = the number of fish in a certain year class at the beginning of the year in area A.
N_{B} = the number of fish in the year class at the beginning of the year in area B.
C_{A} = catch (in number) of the year class throughout the year in area A.
C_{B} = catch (in number) of the year class throughout the year in area B.
E = instantaneous emigration rate from area A to area B.
M = natural mortality (for simplicity it is assumed that M is the same for area A and area B. One could, however, easily introduce separate natural mortalities for area A and area B in the equations developed below).

At any time t within the year the number of fish in the year class in area A is given by

$$N_{\mathrm{A},t} = N_{\mathrm{A}}\exp[-(M + E + F_{\mathrm{A}})t] \tag{1}$$

and setting $t = 1$ gives the number at the beginning of next year. The catch during the year in area A is then given by

$$C_{\mathrm{A}} = F_{\mathrm{A}}N_{\mathrm{A}}\int_0^1 \exp[-(M + E + F_{\mathrm{A}})t]dt =$$
$$= \frac{N_{\mathrm{A}}F_{\mathrm{A}}}{F_{\mathrm{A}} + M + E}\{1 - \exp[-(F_{\mathrm{A}} + M + E)]\} \tag{2}$$

Equations (1) and (2) are simply the common Beverton and Holt equations with M substituted by $M+E$. Accordingly a VPA may be run for area A by substituting M by $M + E$ in the VPA formulae.

The number of fish which migrate into area B in any infinitesimal time interval dt_1 is given by

$$dN_{\mathrm{AB},t_1} = EN_{\mathrm{A}}\exp[-(M + E + F_{\mathrm{A}})t_1]dt_1$$

Of these

$$dN_{\mathrm{AB},t_1}\exp[-(M + F_{\mathrm{B}})(t - t_1)]$$

survives until time $t(t > t_1)$. Therefore the number of fish in area B at time t which have emigrated from area A during the year is given by

$$\begin{aligned} N_{\mathrm{AB},t} &= \int_0^t EN_{\mathrm{A}}\exp[-(M + E + F_{\mathrm{A}})t_1] \times \\ &\quad \times \exp[-(M + F_{\mathrm{B}})(t - t_1)]dt_1 \\ &= EN_{\mathrm{A}}\exp[-(M + F_{\mathrm{B}})t] \times \\ &\quad \times \int_0^t \exp[-(M + E + F_{\mathrm{A}})t_1] \times \\ &\quad \times \exp[(M + F_{\mathrm{B}})t_1]dt_1 \\ &= EN_{\mathrm{A}}\exp[-(M + F_{\mathrm{B}})t] \times \\ &\quad \times \int_0^t \exp[-(E + F_{\mathrm{A}} - F_{\mathrm{B}})t_1]dt_1 \end{aligned}$$

$$= \frac{EN_{\mathrm{A}}}{E+F_{\mathrm{A}}-F_{\mathrm{B}}}\{\exp[-(M+F_{\mathrm{B}})t] - \exp[-(M+E+F_{\mathrm{A}})t]\}$$

In addition

$$N_{\mathrm{B}}\exp[-(M+F_{\mathrm{B}})t]$$

of the fish which were in area B at the beginning of the year will have survived until time t.

Thus, the number of fish in area B at time t is given by

$$N_{\mathrm{B},t} = N_{\mathrm{B}}\exp[-(M+F_{\mathrm{B}})t] + \frac{EN_{\mathrm{A}}}{E+F_{\mathrm{A}}-F_{\mathrm{B}}} \times \{\exp[-(M+F_{\mathrm{B}})t] - \exp[-(M+E+F_{\mathrm{A}})t]\} \qquad (3)$$

and setting $t = 1$ one gets the number at the beginning of the next year.

The case when $E + F_{\mathrm{A}} = F_{\mathrm{B}}$ needs special treatment. It may be shown, either by replacing $E + F_{\mathrm{A}}$ with F_{B} in the integration carried out above, or by studying the limit value of (3) when $E + F_{\mathrm{A}}$ approaches F_{B}, that Equation (3) in this case reduces to

$$N_{\mathrm{B},t} = N_{\mathrm{B}}\exp[-(M+F_{\mathrm{B}})t] + EN_{\mathrm{A}}\exp[-(M+F_{\mathrm{B}})t]t \qquad (3a)$$

Equation (3) shows that the resultant total "mortality", $-\ln(N_{i+1}/N_i)$, throughout the year in area B is given by

$$-\ln\left[\exp[-(M+F_{\mathrm{B}})] + \frac{N_{\mathrm{A}}}{N_{\mathrm{B}}}\frac{E}{E+F_{\mathrm{A}}-F_{\mathrm{B}}} \times \{\exp[-(M+F_{\mathrm{B}})] - \exp[-(M+E+F_{\mathrm{A}})]\}\right]$$

For high values of E and $N_{\mathrm{A}}/N_{\mathrm{B}}$, and low values of F_{B}, this "mortality" may become negative.

The catch throughout the year in area B is given by

$$C_{\mathrm{B}} = \int_0^1 F_{\mathrm{B}}N_{\mathrm{B},t}\,dt$$

which, by using Equation (3), is equal to

$$C_{\mathrm{B}} = \int_0^1 F_{\mathrm{B}}\Big[N_{\mathrm{B}}\exp[-(M+F_{\mathrm{B}})t] + \frac{EN_{\mathrm{A}}}{E+F_{\mathrm{A}}-F_{\mathrm{B}}}\{\exp[-(M+F_{\mathrm{B}})t] - \exp[-(M+E+F_{\mathrm{A}})t]\}\Big]dt$$

The solution of this integral may be written as

$$C_{\mathrm{B}} = \frac{N_{\mathrm{B}}F_{\mathrm{B}}}{M+F_{\mathrm{B}}}\{1-\exp[-(M+F_{\mathrm{B}})]\} + \frac{N_{\mathrm{A}}EF_{\mathrm{B}}}{E+F_{\mathrm{A}}-F_{\mathrm{B}}}\left\{\frac{1-\exp[-(M+F_{\mathrm{B}})]}{M+F_{\mathrm{B}}} - \frac{1-\exp[-(M+E+F_{\mathrm{A}})]}{M+E+F_{\mathrm{A}}}\right\} \qquad (4)$$

As for Equation (3) the case when $E + F_{\mathrm{A}}$ is equal to F_{B} needs special treatment. It may be shown, either by studying the limit value of (4) when $E + F_{\mathrm{A}}$ approaches F_{B}, or by integrating (3a) instead of (3), that Equation (4) in this case reduces to

$$C_{\mathrm{B}} = \frac{N_{\mathrm{B}}F_{\mathrm{B}}}{M+F_{\mathrm{B}}}\{1-\exp[-(M+F_{\mathrm{B}})\} + \frac{N_{\mathrm{A}}EF_{\mathrm{B}}}{(M+F_{\mathrm{B}})^2}\{1-(1+M+F_{\mathrm{B}}) \times \exp[-(M+F_{\mathrm{B}})]\} \qquad (4a)$$

As explained above, the usual VPA technique may be used to calculate stock sizes and fishing mortalities backwards in area A if E is known, setting $M' = M + E$. Knowing then F_{A} and N_{A}, it is possible to use Equations (3) and (4) in a way similar to the VPA technique to calculate N_{B} and F_{B} backwards year for year because, knowing $N_{\mathrm{B},i+1}$ and $C_{\mathrm{B},i}$, the only unknowns are $N_{\mathrm{B},i}$ and $F_{\mathrm{B},i}$.

It can be shown that Equations (3) and (4) imply

$$C_{\mathrm{B},i}/N_{\mathrm{B},i+1} = a_i - b_iN_{\mathrm{A},i}/N_{\mathrm{B},i+1} \qquad (5)$$

where

$$a_i = F_{\mathrm{B},i}[\exp(M+F_{\mathrm{B},i})-1]/(M+F_{\mathrm{B},i}) \qquad (6)$$

is a function of $F_{\mathrm{B},i}$ and M, and

$$b_i = \frac{EF_{\mathrm{B},i}}{E+F_{\mathrm{A},i}-F_{\mathrm{B},i}}\left\{\frac{1-\exp[-(M+E+F_{\mathrm{A},i})]}{M+E+F_{\mathrm{A},i}} - \frac{\exp[-(M+E+F_{\mathrm{A},i})][\exp(M+F_{\mathrm{B},i})-1]}{M+F_{\mathrm{B},i}}\right\} \qquad (7)$$

is a function of $F_{\mathrm{A},i}$, $F_{\mathrm{B},i}$, E and M. In the special case when $E + F_{\mathrm{A},i} = F_{\mathrm{B},i}$ (7) reduces to

$$b_i = \frac{EF_{\mathrm{B},i}}{M+F_{\mathrm{B},i}}\left\{1 - \frac{1-\exp[-(M+F_{\mathrm{B},i})]}{M+F_{\mathrm{B},i}}\right\} \qquad (7a)$$

As expected $b = 0$ when $E = 0$ and Equation (5) reduces to

$$C_{\mathrm{B},i}/N_{\mathrm{B},i+1} = a_i = F_{\mathrm{B},i} \times [\exp(M+F_{\mathrm{B},i})-1]/(M+F_{\mathrm{B},i})$$

as in the ordinary VPA.

When $N_{\mathrm{A},i}$, $F_{\mathrm{A},i}$, $N_{\mathrm{B},i+1}$ and $C_{\mathrm{B},i}$ are known, $F_{\mathrm{B},i}$ can be found from (5) either by iteration or by reference to tables of a and b. Having estimated $F_{\mathrm{B},i}$, $N_{\mathrm{B},i}$ is known from (3) and one can proceed further one year backwards. Because b is a function of both F_{A}, F_{B}, M and E the tables necessary will be much more voluminous than in an ordinary VPA

Table 1. VPA analysis for area A and B taking into account an instantaneous emigration rate $E = 0{\cdot}2$ from A to B. $M = 0{\cdot}2$

Age (i)	$C_{A,i}$	$C_{B,i}$	$F_{A,i}$	$N_{A,i}$	$\frac{C_{B,i}}{N_{B,i+1}}$	$\frac{N_{A,i}}{N_{B,i+1}}$	$F_{B,i}$ estimated	$F_{B,i}$ true	$N_{B,i}$
8..............	1·865	10·30	0·4	6·772			0·4	(0·4)	33·67
7..............	2·56	24·77	0·266	13·18	0·7357	0·3914	0·52	(0·515)	66·47
6..............	13·08	24·59	0·583	35·23	0·3699	0·5300	0·29	(0.295)	102·9
5..............	12·97	60·15	0·260	68·16	0·5845	0·6623	0·43	(0·435)	179·8
4..............	73·31	169·3	0·619	188·8	0·9416	1·050	0·63	(0·630)	377·9
3..............	94·09	160·8	0·337	394·6	0·4255	1.044	0·34	(0·339)	576·8
2..............	201·5	189·3	0·344	830·4	0·3282	1·440	0·28	(0·277)	786·1
1..............	637·4	296·6	0·479	2 000·0	0·3773	2·544	0·33	(0·328)	997·9

Table 2. Values of a and b in equation (5) for various values of F_A and F_B. $M = E = 0{\cdot}2$

F_B	a	Values of b at different values of F_A								
		0·25	0·30	0·35	0·40	0·45	0·50	0·55	0·60	0·65
0·25	0·3157	0·0190	0·0184	0·0178	0·0173	0·0167	0·0162	0·0157	0·0152	0·0148
0·26	0·3301	0·0198	0·0192	0·0186	0·0180	0·0175	0·0169	0·0164	0·0159	0·0154
0·27	0·3447	0·0207	0·0200	0·0194	0·0188	0·0182	0·0176	0·0171	0·0166	0·0160
0·28	0·3594	0·0215	0·0208	0·0202	0·0195	0·0189	0·0183	0·0178	0·0172	0·0167
0·29	0·3742	0·0223	0·0216	0·0210	0·0203	0·0197	0·0191	0·0185	0·0179	0·0174
0·30	0·3892	0·0232	0·0225	0·0218	0·0211	0·0204	0·0198	0·0192	0·0186	0·0180
0·31	0·4044	0·0241	0·0233	0·0226	0·0218	0·0212	0·0205	0·0199	0·0193	0·0187
0·32	0·4197	0·0249	0·0241	0·0234	0·0226	0·0219	0·0212	0·0206	0·0199	0·0193
0·33	0·4352	0·0258	0·0250	0·0242	0·0234	0·0227	0·0220	0·0213	0·0206	0·0200
0·34	0·4508	0·0267	0·0258	0·0250	0·0242	0·0234	0·0227	0·0220	0·0213	0·0207
0·35	0·4666	0·0275	0·0267	0·0258	0·0250	0·0242	0·0235	0·0227	0·0220	0·0214
0·36	0·4826	0·0284	0·0275	0·0266	0·0258	0·0250	0·0242	0·0235	0·0227	0·0220
0·37	0·4987	0·0293	0·0284	0·0275	0·0266	0·0258	0·0250	0·0242	0·0235	0·0227
0·38	0·5150	0·0302	0·0292	0·0283	0·0274	0·0266	0·0257	0·0249	0·0242	0·0234
0·39	0·5314	0·0311	0·0301	0·0292	0·0282	0·0274	0·0265	0·0257	0·0249	0·0241
0·40	0·5481	0·0320	0·0310	0·0300	0·0291	0·0282	0·0273	0·0264	0·0256	0·0248
0·41	0·5649	0·0329	0·0319	0·0309	0·0299	0·0290	0·0281	0·0272	0·0263	0·0255
0·42	0·5819	0·0338	0·0328	0·0317	0·0307	0·0298	0·0288	0·0279	0·0271	0·0262
0·43	0·5990	0·0348	0·0337	0·0326	0·0316	0·0306	0·0296	0·0287	0·0278	0·0270
0·44	0·6163	0·0357	0·0346	0·0335	0·0324	0·0314	0·0304	0·0295	0·0286	0·0277
0·45	0·6338	0·0366	0·0355	0·0344	0·0333	0·0322	0·0312	0·0302	0·0293	0·0284
0·46	0·6515	0·0376	0·0364	0·0352	0·0341	0·0331	0·0320	0·0310	0·0301	0·0291
0·47	0·6694	0·0385	0·0373	0·0361	0·0350	0·0339	0·0328	0·0318	0·0308	0·0299
0·48	0·6874	0·0395	0·0382	0·0370	0·0359	0·0347	0·0336	0·0326	0·0316	0·0306
0·49	0·7057	0·0405	0·0392	0·0379	0·0367	0·0356	0·0345	0·0334	0·0323	0·0313
0·50	0·7241	0·0414	0·0401	0·0388	0·0376	0·0364	0·0353	0·0342	0·0331	0·0321
0·51	0·7427	0·0424	0·0411	0·0398	0·0385	0·0373	0·0361	0·0350	0·0339	0·0328
0·52	0·7615	0·0434	0·0420	0·0407	0·0394	0·0381	0·0369	0·0358	0·0347	0·0336
0·53	0·7805	0·0444	0·0430	0·0416	0·0403	0·0390	0·0378	0·0366	0·0355	0·0344
0·54	0·7997	0·0454	0·0439	0·0425	0·0412	0·0399	0·0386	0·0374	0·0363	0·0351
0·55	0·8191	0·0464	0·0449	0·0435	0·0421	0·0408	0·0395	0·0383	0·0371	0·0359
0·56	0·8387	0·0474	0·0459	0·0444	0·0430	0·0417	0·0403	0·0391	0·0379	0·0367
0·57	0·8585	0·0484	0·0469	0·0454	0·0439	0·0426	0·0412	0·0399	0·0387	0·0375
0·58	0·8785	0·0495	0·0479	0·0463	0·0449	0·0435	0·0421	0·0408	0·0395	0·0383
0·59	0·8987	0·0505	0·0489	0·0473	0·0458	0·0444	0·0430	0·0416	0·0403	0·0391
0·60	0·9192	0·0515	0·0499	0·0483	0·0467	0·0453	0·0438	0·0425	0·0411	0·0399
0·61	0·9398	0·0526	0·0509	0·0493	0·0477	0·0462	0·0447	0·0433	0·0420	0·0407
0·62	0·9606	0·0536	0·0519	0·0503	0·0487	0·0471	0·0456	0·0442	0·0428	0·0415
0·63	0·9817	0·0547	0·0529	0·0512	0·0496	0·0480	0·0465	0·0451	0·0436	0·0423
0·64	1·0029	0·0558	0·0540	0·0522	0·0506	0·0490	0·0474	0·0459	0·0445	0·0431
0·65	1·0244	0·0568	0·0550	0·0533	0·0516	0·0499	0·0483	0·0468	0·0453	0·0439

The procedure may be illustrated by a numerical example. Suppose $M = E = 0{\cdot}2$ and that the catches of a year class at different ages in area A and B are as given in the left hand columns of Table 1. In the next two columns are given the results of an ordinary VPA for area A (including E in the natural mortality), assuming a fishing mortality of 0·4 at age 8. If this fishing mortality also is assumed for area B at age 8, Equation (3) gives a value of 33·67 for the stock size. Table 1 is then complete for age 8, and one can proceed to age 7 by calculating $C_{B,7}/N_{B,8}$ and $N_{A,7}/N_{B,8}$ and then utilize Equation (5). Values of a and b in Equation (5) are given in Table 2 for the case when $M = E = 0{\cdot}2$. Values for b are tabulated for a number of F_A-values in steps of 0·05 for each F_B. In our examples is $F_{A,7} = 0{\cdot}266$, and the nearest F_A-value in Table 2 is 0·25. To get $a - bN_{A,7}/N_{B,8} = 0{\cdot}7357$ it is readily seen that $F_{B,7}$ has to lie between 0·51 and 0·52. $F_B = 0{\cdot}51$ gives the value $0{\cdot}7427 - (0{\cdot}0424 \times 0{\cdot}3914) = 0{\cdot}7261$, while $F_B = 0{\cdot}52$ gives $0{\cdot}7615 - (0{\cdot}0434 \times 0{\cdot}3914) = 0{\cdot}7445$. If one wants only two decimals, the value 0·52 thus gives the best fit. If a higher degree of precision is required, one can of course interpolate between the values in Table 2. Having estimated $F_{B,7}$, $N_{B,7}$ can be calculated from Equation (3) and one can proceed to age 6. All values for F_B and N_B in Table 1 are estimated by this procedure. The catches in Table 1 were generated by known fishing mortalities. The true values for the fishing mortalities in area B are given in parenthesis, and it is seen that all estimated F_B-values are correct in the second decimal.

If one wants to go through the procedure described above to study a stock consisting of several year classes over a number of years, this will be quite laborious and time consuming, especially if one wants to try various values of starting fishing mortality, natural mortality or emigration rate. Any extensive use of the technique therefore has to be based on computer programs which solve the equations by iteration.

Equations (1) to (4) make it possible to see how the results of a VPA, which do not take any account of the migration, would depart from the true values of stock sizes and fishing mortalities. For illustration the following values for the parameters were chosen:

$M = 0{\cdot}2$

$E = 0$ for age-groups 1 and 2, $E = 0{\cdot}2$ for 3 years old and older fish

$F_A = 0{\cdot}3 \qquad F_B = 0{\cdot}6$

$N_{A,\,\text{age }1} = 1500 \qquad N_{B,\,\text{age }1} = 3000$

Catches and stock sizes of the different age-groups were calculated for each area separately using the Equations (1) to (4). Catches and stock sizes in the

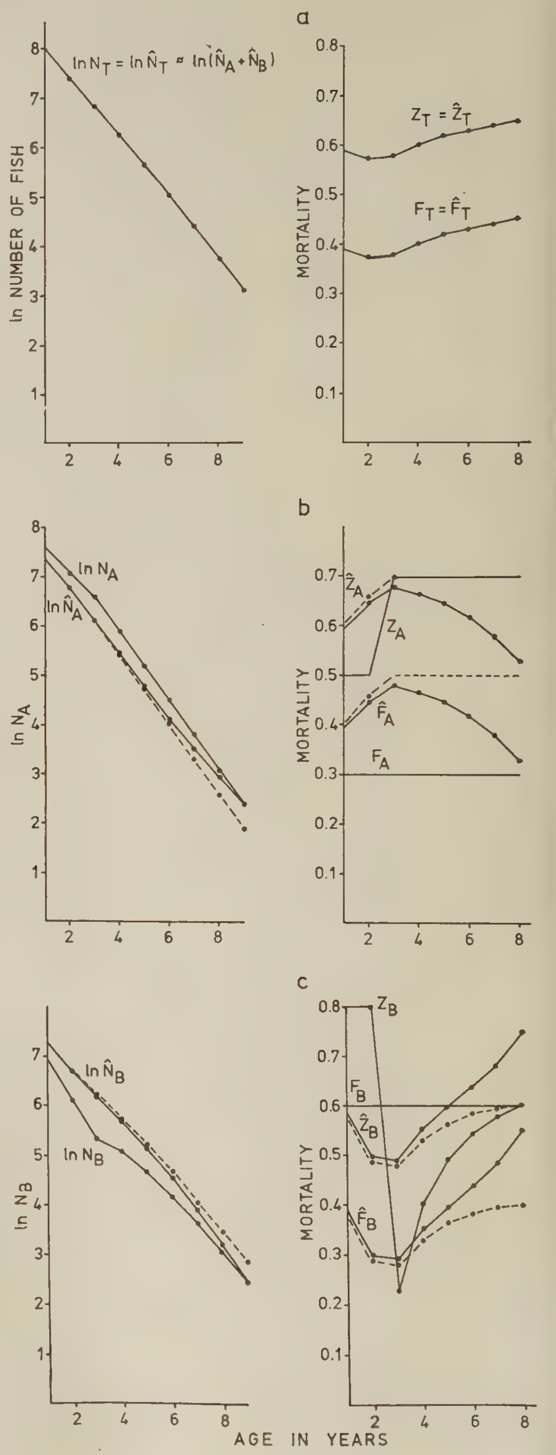

Figure 9. (a), logarithm of total number of fish ($\ln N_T$), total mortality (Z_T) and fishing mortality (F_T) at different ages for areas A and B combined. (b) and (c), logarithm of estimated number of fish ($\ln \hat{N}$), estimated total mortality ($\hat{Z}$) and estimated fishing mortality ($\hat{F}$) at different ages from VPA for area A (b) and area B (c) (whole line: $\hat{N}_9 = N_9$, broken line: $\hat{Z}_8 = Z_8$) together with true values.

two areas were then summed to give catches and stock sizes for the areas combined. For each area and the areas combined total "mortality" on age group $i(Z_i)$ was calculated as $-\ln N_{i+1}/N_i$. The fishing mortality on age group $i(F_i)$ for the areas combined was calculated as $Z_i - M = Z_i - 0{\cdot}2$.

Using then the calculated catches three different VPA's were run, one for each of the areas and one for the areas combined. The true value was chosen as starting value for the stock size of the oldest age-group (the 9 years old). In addition one VPA was run for each area, using a starting stock size calculated from the true total "mortality" and catches of 8 years old. In all runs a natural mortality of 0·2 was used. The results are shown in Figure 9a–c.

As expected the combined VPA gave results almost exactly equal to the true values (Fig. 9a). Some negligible differences in the decimals have the following explanation. In VPA it is assumed that fishing mortality is evenly distributed over the year (cf. section 5). Here this is not the case for the areas combined. The fishing mortality gradually changes according to changes in the ratio $N_{B,t}/N_{A,t}$. For ages 1 and 2, $N_{B,t}/N_{A,t}$ decreases during the year because of higher total mortality in area B than in area A, and as a result F gradually decreases, because $F_B > F_A$. Therefore VPA slightly overestimates N_i/N_{i+1} for these age groups (cf. section 5). For the older age-groups the contrary is true because of the continuous migration from area A to area B which results in a gradual increase in the ratio $N_{B,t}/N_{A,t}$ during the year[2].

The results of the separate VPA's showed that

$$\hat{N}_A + \hat{N}_B \approx N_A + N_B$$

This is also what should be expected as VPA essentially estimates stock size of a year class by summing the catches of the different age groups, correcting the catches of each age group for the natural mortality this age group has experienced. In the constructed example M is equal in the two areas and it therefore should not matter what area the catch is taken in when one corrects for natural mortality. However, for a given M, the relation between stock sizes in two successive years may be written as (cf. section 5)

$$N_i = C_i \exp(kM) + N_{i+1} \exp(M)$$

k will depend on F_i, or on how the catch is distributed over the year. k will be correctly estimated in the VPA if fishing mortality is evenly distributed over the year and there is no migration from or to the area during the year. However, in our example the migration will disturb this in the separate VPA's, and therefore $\hat{N}_A + \hat{N}_B$ will not be exactly equal to $N_A + N_B$.

The VPA for area A (Fig. 9b) underestimates stock size and overestimates fishing mortality because the natural mortality used does not include emigration and therefore is too low. The estimated total mortality Z_A gradually approaches the correct value as the year class is backcalculated until age 3. For age groups 2 and 1 the true mortality Z_A decreases from 0·7 to 0·5 because these age groups do not emigrate, and $\hat{Z}_A$ strongly overestimates Z_A. If instead of assuming $\hat{N}_{A,9} = N_{A,9}$ in the VPA, one put $\hat{Z}_{A,8} = Z_{A,8}$, the VPA correctly estimate Z for agegroups 3–8, but constantly overestimate F to 0·5 compared with the true value of 0·3. This is in agreement with what was said in section 4(i) concerning the case when Z is constant, Z last year correct, but M is wrong in the VPA.

As expected, a VPA assuming $M = 0{\cdot}4$ ($M = 0{\cdot}2 + E$) for age-groups 3–8 and $M = 0{\cdot}2$ for ages 1 and 2 gave results identical to the true values.

The comparison of true values with VPA results for area B (Fig. 9c) is the more interesting part of the exercise. The first interesting feature is that Z_B is less than F_B for ages 3–8, the difference decreasing with age. This means that migration into the area more than compensates natural mortality, or that the resultant "natural" mortality is negative. A VPA assuming a constant (positive) natural mortality will then of course give completely wrong results both for N_B, F_B and Z_B. $\hat{N}_B$ strongly overestimates N_B, and the relative overestimation increases with decreasing age (until age 3). $\hat{Z}_B$ strongly overestimates Z_B (for age 3–8), and $\hat{F}_B$ strongly underestimates F_B. $\hat{Z}_B$ and $\hat{F}_B$ strongly decreases with age until age 3, giving an $\hat{F}_B$ for age group 3 of 0·29 against a true value of 0·6[3]. By assuming $\hat{Z}_8 = Z_8$

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[2] It was demonstrated that by dividing the year into 5 equal parts the VPA analysis gave results closer to the true values, which confirms this explanation. For example, on an annual basis

$$\hat{N}_3/\hat{N}_4 - N_3/N_4 = -0{\cdot}000368$$

while by dividing the year into 5 parts when carrying out the VPA

$$\hat{N}_3/\hat{N}_4 - N_3/N_4 = -0{\cdot}000027$$

[3] An example of a VPA which shows a decreasing F with age (in age groups which normally should be fully recruited to the fishery) is found in Report of the North-Western Working Group (Anon, 1976). The Working Group explained the low estimated fishing mortality on age-groups 4–6 for some year classes of cod at Iceland by immigration from East and southern West Greenland.

instead of $\hat{N}_9 = N_9$, the $\hat{Z}_B$ will be nearer the true value for the older age groups but the errors in $\hat{F}_B$ will increase.

As long as a constant M is assumed in the VPA, the VPA will give a completely wrong picture of the real situation, and the only way to solve the problem is to try to take account of the immigration by utilizing Equations (3)–(4), assuming N_A and F_A already have been estimated by VPA using Equations (1)–(2).

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Age et croissance de *Raja batis* et de *Raja naevus* en Mer Celtique

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L'âge de *R. batis* et de *R. naevus* a été déterminé par lecture des anneaux de croissance inscrits dans les corps vertebraux. 126 spécimens de *R. batis* et 217 de *R. naevus* en provenance de la Mer Celtique ont été examinés. Les observations ont permis la calcul des paramètres de l'équation de croissance:

$$R.\ batis \quad L_t = 254\,[1 - \exp - 0{\cdot}057\,(t + 1{\cdot}63)]$$
$$R.\ naevus \quad L_t = 91{\cdot}64\,[1 - \exp - 0{\cdot}108\,(t + 0{\cdot}46)]$$

Les taux de croissance sont de même ordre que ceux obtenue par Holden (1972) d'expériences de marquage sur trois expèces de raies des eaux britanniques.

Holden, M. J. 1972. J. Cons. int. Explor. Mer, 33: 335–9.

Introduction

La détermination de l'âge des raies est classiquement basée sur l'analyse des anneaux de calcification inscrits dans les pièces squelettiques et Holden and Vince (1973) a justifié l'utilisation de cette méthode chez les sélaciens en montrant qu'il se forme annuellement un seul anneau opaque dans les corps vertébraux de *Raja clavata*.

Plusieurs techniques ont été décrites pour mettre en évidence les anneaux de croissance: coloration à l'hématoxyline (Ishiyama, 1956), imprégnation à la paraffine (Daiberg, 1960), deshydratation suivi d'examen dans l'alcool absolu (Richards et al, 1963), coloration à l'alizarine (Lamarca, 1966), enfin pour les spécimens de grande taille (Aasen, 1963) préconise l'examen aux rayons X.

Méthodes

Trois méthodes de mises en évidence des anneaux de calcification ont été utilisées.

Méthode de Daiberg

Après fixation au formol à 10%, les corps vertébraux sont deshydratés à l'alcool à 95% pendant 4 h, à l'alcool absolu pendant 32 h, au xylène pendant 24 h; ils sont ensuite traités à la paraffine à 60°C pendant 24 h et conservés dans le xylène.

Méthode à l'alizarine

Les trois techniques dérivent de la méthode de Williams (1941) basée sur l'affinité de l'alizarine S pour le calcium.

a) Fixation des corps vertébraux par le formol à 10% pendant 48 h. Traitement à la potasse à 15% pendant 15 à 60 min; potasse à 2% + alizarine pendant 24 à 48 h; potasse à 2% pendant 15 à 60 min; potasse à 2% + glycérine pendant 24 à 48 h. Conservation dans la glycérine pendant 24 à 48 h. Conservation dans la glycérine.

b) Fixation des corps vertébraux à l'alcool à 95° pendant 48 à 96 h. Traitement à la potasse à 1% pendant 24 à 48 h; potasse à 1% + alizarine pendant 24 h; potasse à 1% + glycerine (50 + 50). Conservation dans la glycérine.

c) Traitement par la soude à 0·2% pendant 24 h. Coloration par la soude + alizarine (9 + 1) pendant 24 à 72 h; lavage à l'eau courante 15 min; différientiation par l'eau oxygéné à 3% pendant 24 à 72 h. Conservation dans l'alcool à 70°.

Examen direct sans coloration

a) Plaque mince: après fixation au formol à 10% ou simple séchage, les vertèbres sont sciées selon un plan soit sagittal, soit transversal passant par le milieu du centrum. Les demi vertèbres sont ensuite collées sur une plaque de verre et traitées selon la technique utilisée en géologie pour la préparation des plaques minces c'est-à-dire qu'elles sont usées mécaniquement jusqu'à l'obtention d'une coupe de quelques dixièmes de millimètres d'épaisseur. L'examen se fait par transparence sous loupe binoculaire.

b) Rayons X: les vertèbres sectionnées selon un plan transversal sont exposées aux rayons X selon ce plan.

Quelle que soit la technique utilisée, les vertèbres sont prélevées dans la zone antérieure ou abdominal de la colonne vertèbrale qui semble la plus favorable à ces examens (Daiberg, 1960; Ishiyama, 1956).

L'étude a porté sur des exemplaires récoltés en Mer Celtique; au total 126 spécimens de *R. batis* et 217 de *R. naevus* ont été examinés. Les différentes méthodes de coloration et d'imprégnation ont été appliquées. Leur efficacité est sensiblement équivalente, il existe toujours une forte majorité de vertèbres où les anneaux de croissance sont illisibles. Ainsi 82 individus de *R. batis* et 50 de *R. naevus* seulement ont fournis des indications utilisables.

Pour éliminer le cas échéant les erreurs d'interprétation dans la lecture des anneaux nous avons eu recours à deux méthodes pour déterminer la taille moyenne aux différents âges.

1) La première consiste à calculer directement la moyenne des tailles chez les individus présentant le même nombre d'anneaux de croissance.

2) La deuxième consiste à calculer indirectement cette moyenne en utilisant la relation qui existe entre la taille de la vertèbre, ici le diamètre, et la longueur du poisson. De la mesure du diamètre des anneaux inscrits dans les corps vertèbraux on déduit la longueur du spécimen au moment de leur formation.

Les mensurations sont faites au micromètre oculaire selon l'axe horizontal des vertèbres, celles-ci présentant un léger aplatissement dorso-ventral.

Résultats

Relation entre le diamètre des vertèbres et la longueur totale

Les observations sont converties en millimètres; la longueur totale est exprimée en centimètres.

a) *R. batis*

Les vertèbres de 117 exemplaires, 40 ♂ et 77 ♀ ont été mesurées. Le calcul de l'équation de la droite de régression et de l'indice de corrélation (intervalle à 5%) a donné les résultats suivants:

$$\begin{aligned} \male \quad & Y = 0{\cdot}088X - 1{\cdot}68, \quad r = 0{\cdot}990 \\ \female \quad & Y = 0{\cdot}096X - 1{\cdot}66, \quad r = 0{\cdot}985 \\ \male + \female \quad & Y = 0{\cdot}094X - 1{\cdot}41, \quad r = 0{\cdot}985 \end{aligned}$$

b) *R. naevus*

Les vertèbres de 215 exemplaires, 83 ♂ et 132 ♀ ont été mesurées. Le calcul de la droite de regression et de l'indice de corrélation a donné les résultats suivants:

$$\begin{aligned} \male \quad & Y = 0{\cdot}100X - 0{\cdot}520, \quad r = 0{\cdot}978 \\ \female \quad & Y = 0{\cdot}101X - 0{\cdot}507, \quad r = 0{\cdot}962 \\ \male + \female \quad & Y = 0{\cdot}102X - 0{\cdot}533, \quad r = 0{\cdot}968 \end{aligned}$$

Dans les deux espèces les paramètres de l'équation ne sont pas significativement différents dans les deux sexes; la corrélation entre les deux variables est satisfaisante ce qui nous a permis de ne pas séparer les sexes et d'utiliser simultanément la totalité de l'effectif tout en sachant que le dimorphisme sexuel de taille observé chez *R. batis* se traduit probablement, dans les équations de croissance, par des paramètres de valeurs différentes.

Détermination de l'équation de croissance selon le modèle de von Bertalanffy

Quatre-vingt-deux spécimens de *R. batis* et 50 de *R. naevus* présentaient des anneaux de croissance lisibles (Tableau 1).

L'observation des données âge-longueur totale indique que la croissance des deux espèces peut-être raisonnablement décrite par une équation de croissance de type asymptotique. C'est pourquoi nous avons choisi d'utiliser la loi de croissance dite de von Bertalanffy. L'estimation des paramètres a été obtenue en appliquant le programme écrit par Tomlinsom (Abramson, 1971) adapté par A. Laurec pour l'ordinateur C II 10070 du Centre Océanologique de Bretagne (Plouzané, Finistère).

Les paramètres de l'équation $L_t = L_\infty \{1 - \exp[-K(t - t_0)]\}$ leurs erreurs standards estimées à partir de la variance résiduelle sont donnés dans Tableau 2.

Les estimations de L_∞ sont cohérentes avec les tailles maximales enrégistrées pour ces deux espèces en Mer Celtique (235 et 72 cm respectivement). Les valeurs de K sont de même grandeur que celles calculées par Holden (1972) pour *R. brachyura*, *R. clavata* et *R. montagui*. Or les résultats de cet auteur sont basés sur des expériences de marquage et ne sont donc pas entachés d'erreurs de lecture. Il est par conséquent intéressant d'aboutir à des conclusions semblables à l'aide d'une méthode où l'interprètation joue un rôle non négligeable[1].

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[1] On peut simplement noter que pour les ♂ de *R. clavata* l'estimation de L_∞ faite par Holden (1972), 85·6 cm, est nettement inférieur à la taille maximale observée en Mer Celtique, 108 cm (Du Buit, 1974).

Tableau 1. Valeurs expérimentales et valeurs calculées des tailles moyennes aux différents âges pour *R. batis* et *R. naevus* (moyennes théoriques obtenues à partir de l'équation de von Bertalanffy; LT graphiques par la méthode de retrocalcul basée sur le diamètre des vertèbres).

Nombre d'anneaux	LT cm	LT cm Moyennes		Diamètre vertèbre mm	LT cm graphique
		expérimentale	théorique		
	R. batis				
1	31, 35	33		1·88	35
2	40, 44 (2), 45, 46, 49, 50, 53	46·38	47·41	2·64	43
3	51, 53, 54, 57 (2), 58, 59, 61, 65, 67	58·20	58·84	3·62	53
4	67, 70 (2), 72, 73, 74 (2), 85	73·12	69·64	4·36	62
5	69, 73, 74, 78, 80 (2), 85, 92	80·12	79·84	5·26	71
6	85, 89 (2), 90, 92 (2), 94, 97	91·0	89·47	6·60	86
7	92, 94, 97, 99	95·20	98·57	7·30	93
8	110, 110, 110, 113	110·75	107·17	7·60	96
9	110 (4), 117, 120	114·50	115·29	8·60	106
10	117, 118, 119, 120, 121, 123 (2), 130	120·12	122·96	9·30	114
11	120, 132, 133, 138	130,75	130·20	9·90	120
12	127, 133, 138	132·67	137·04	–	–
13	145	145	143·51	–	–
14	155, 156	155·5	149·62	–	–
15	160	160	155·38	–	–
16		–	160·84	–	–
17	180, 186	183	165·99	–	–
18		–	170·85	–	–
19		–	175·44	–	–
20	202	202	183·87	–	–
21		–	187·74	–	–
22	213	213	187·74	–	–
23		–	191·40	–	–
	R. naevus				
0	13 (2), 14, 16, 16·5	14·50	13·48	–	–
1	17, 17.5, 20	18·17	21·51	1·40	20
2	29, 31 (2)	30·33	28·73	2·00	26
3	36	36	35·20	2·46	30
4	39, 40, 41, 44, 45	41·80	41·01	3·20	37
5	42, 42·5, 43, 46, 47, 49	44·83	46·21	3·78	43
6	45, 46, 50 (2), 54, 55	50·00	50·89	4·42	49
7	54 (3), 57, 58, 59	46·00	55·08	4·80	53
8	60 (2), 62	60·67	58·84	5·20	58
9	62 (3)	62·00	62·21	5·78	62·5
10	64 (2), 65, 67 (2), 68	65·71	65·24	6·02	65
11	67	67·00	67·96	–	–
12	68, 69	68·5	70·39	–	–

Tableau 2. Valeurs estimées des paramètres de l'équation de croissance de *R. batis* et *R. naevus*.

Espèces	L_∞ cm	K	t_0 année
R. batis	253·73	0·0570	−1·629
erreurs std	29·08	0·0106	0·294
R. naevus	91·64	0·1085	−0·465
erreurs std	5·52	0·0130	0·181

La représentation graphique de ces deux équations est donnée sur la Figure 1. On remarquera que l'âge des 4 plus grands spécimens a été nettement sous-estimé (erreur sur la détermination du nombre d'anneaux), les considérér comme exacts nous obligerait à adopter une L_∞ égale à 438 cm ce qui serait sans aucune relation avec la réalité.

La croissance de ces deux expèces diffère sur deux points essentiels:

1. l'accroissement annuel nettement plus important chez *R. batis* que chez *R. naevus*: 12·80; 12·11; 11·4 chez la première au lieu de 8; 7·22; 6·47 cm chez la deuxième.
2. la longévité beaucoup plus grande chez *R. batis*. Ainsi les tailles maximale enrégistrées correspondraient à des individus âgés d'une cinquantaine d'années chez *R. batis* et de treize à quatorze ans chez *R. naevus*.

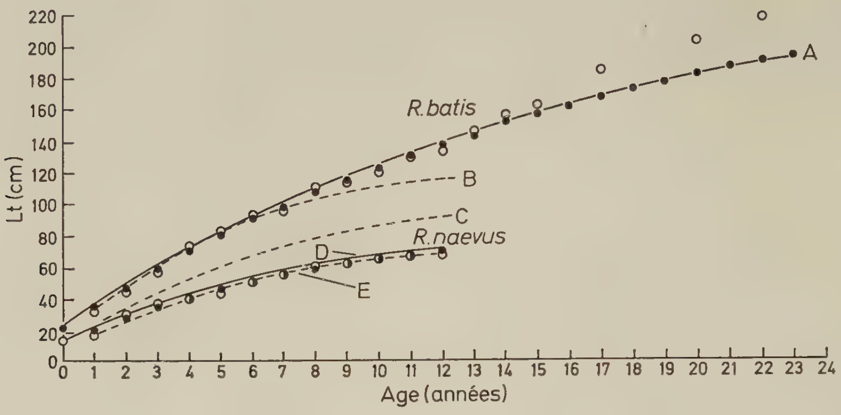

Figure 1. Courbes de croissance de *Raja batis* (A) et *R. naevus* (B). Comparaison avec les résultats obtenus par Holden (1972) pour *R. brachyura* (C), *R. clavata* (D) et *R. montagui* (E).

Comparaison des résultats obtenus par les deux méthodes décrites

Au de là d'une dizaine d'années la mesure du diamètre des anneaux vertèbraux devient impossible chez les deux espèces étudiées. La comparison sera donc limitée à cette période (Tableau 1).

Dans les deux espèces il existe un décalage entre les deux séries de valeurs de LT:

chez *R. batis*, la méthode par rétrocalcul fait apparaître au cours des quatre premières années un anneau qui persiste par la suite;

chez *R. naevus*, le nombre d'anneaux est identique, seul l'accroissement annuel différe durant les sept premières années.

Dans un cas comme dans l'autre, les variations enrégistrées sont sans doute imputables à une imprécision dans la mensuration des anneaux; leurs contours sont parfoits diffus, voire incomplets (on mesure alors leur rayon ce qui introduit un risque d'erreur supplémentaire, le centre de la vertèbre n'étant marqué par aucun repère précis). Il est difficile dans ces conditions d'atteindre un degré de précision comparable à celui d'une numération.

Malgré cet inconvenient, la cohésion des résultats et le fait qu'ils soient de même ordre que ceux obtenus par Holden (1972) confirme la lenteur de la croissance des raies. On constate également que l'âge de la maturité sexuelle se situe chez les cinq expèces européennes étudiées jusqu'à présent, entre 9 et 12 ans quelle que soit leur longévité (Tableau 3).

Ces deux facteurs, croissance extrèmement lente et première maturité à un âge avancé auxquels s'ajoute une fécondité assez basse (Holden et al, 1971) concourent à créer une situation inquiétante pour l'exploitation des stocks des raies de la Mer Celtique.

Tableau 3. Age de première maturité sexuelle et longévité de cinq espèces de raies européennes.

Espèces	Age 1 ère maturité ans	Age maximal ans	
R. batis	11	50	
R. naevus	9	13–14	
R. brachuyra	9	15–20	Holden (1972)
R. clavata..........	12	20	Holden (1972)
R. montagui........	11	18	Holden (1972)

Des deux expèces *R. batis* est évidemment la plus vulnérable et les quantités débarquées par les chalutiers de Concarneau en 1975 représentent seulement 21% des captures réalisées en 1965 dans la même zone de pêche, 190 t au lieu de 900 t.

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Studies on the biology of larval nematodes from the musculature of cod and whiting in Scottish waters

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A total of 1841 cod and 2543 whiting from Scottish waters were examined for the presence of larval nematodes within the musculature. Larval *Phocanema* were common in the musculature of cod from the west coast of Scotland but rare in fish from the central northern North Sea. Larval *Anisakis* were most abundant in the musculature of cod and whiting from offshore northern North Sea areas but were much less common in other areas. *Phocanema* occurred only very occasionally in whiting. *Anisakis* and *Phocanema* rarely occurred together in the musculature of individual cod. Observed variations in infections of fish are possibly due to differences in the geographical distribution of the invertebrate and vertebrate hosts of the parasites. There has apparently been a large increase in the infection of cod and whiting with larval nematodes within the last twenty years probably due mainly to a greater abundance of *Anisakis*.

Infection with larval nematodes increased with age and length of the fish. Most *Anisakis* from the musculature were found in the hypaxial muscles whereas a much larger proportion of *Phocanema* occurred in the epaxials. In whiting over half the total burden of *Anisakis* were found in the musculature rather than the viscera but in cod most larvae occurred in the latter site. There was a significant positive correlation between numbers of *Anisakis* in the viscera and musculature of whiting but not of cod. *Phocanema* was found in a number of fish species which may act as a source of infection for cod.

Introduction

Third-stage larvae of the anisakid nematodes *Phocanema* (= *Terranova* = *Porrocaecum*) *decipiens* (Krabbe, 1878) and *Anisakis* sp. occur commonly in the musculature of cod (*Gadus morhua*) in the North Atlantic. *Anisakis* sp. also occurs in the musculature of whiting (*Merlangius merlangus*) in this area. The unaesthetic appearance and potential human health hazard of these parasites are a source of continued concern to the fishing industry.

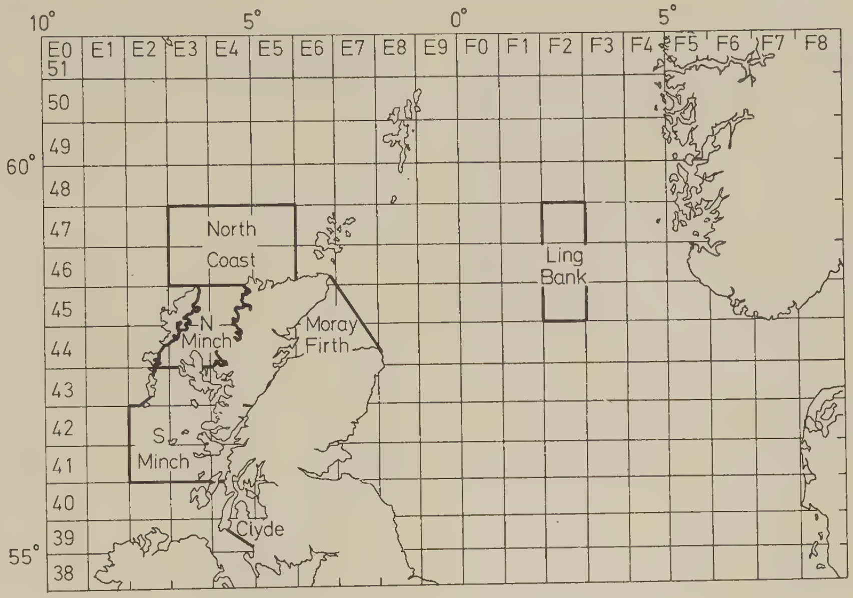
Records of larval nematodes in cod from Scottish waters were reviewed by Rae (1963) with evidence of a considerable increase in the extent of infection of fish since 1945. Further increases in infection apparently occurred between 1962 and 1970 (Rae, 1972). According to Rae (1963) most of the larval nematodes found in cod were *Phocanema*, with relatively few *Anisakis*. Subsequently Rae (1972) suggested that the apparent rise in infection level of cod from offshore grounds since 1962 may be due to an increase in the abundance of larval *Anisakis*. This view was supported by Young (1972) who found that larval *Anisakis* were more abundant than *Phocanema* in cod from the North Sea, especially in offshore areas.

Young (1972) showed that in British waters the grey seal, *Halichoerus grypus* (Fabricius, 1791), is the major final host of *P. decipiens* with cetaceans as the major final hosts of *Anisakis*. Euphausiid crustaceans are probably the most important intermediate hosts of *Anisakis* in British waters (Smith, 1971). The intermediate hosts of *Phocanema* are unknown. Many species of fish can act as transport or paratenic hosts for both parasites.

Larval *Anisakis* obtained from cod and whiting during the present study morphologically resembled the third stage larvae designated *Anisakis* sp. larva (1) by Berland (1961). Such larvae were reared *in vitro* to the adult stage by Van Banning (1971) and identified as *Anisakis simplex* (Rudolphi, 1809; det. Krabbe, 1878) by Pippy and Van Banning (1975). This report presents further information on the occurrence and biology of larval *Phocanema* and *Anisakis* in cod and whiting in Scottish waters.

Materials and methods

Cod and whiting samples were obtained from commercial trawl and seine net catches from 1971 until 1974. Areas in the North Sea and to the west and north of Scotland were sampled (Figs 1 and 2). A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North Coast
Ling Bank
N Minch
Moray Firth
S. Minch
Clyde

Figure 1. Areas from which cod were examined for larval nematodes.

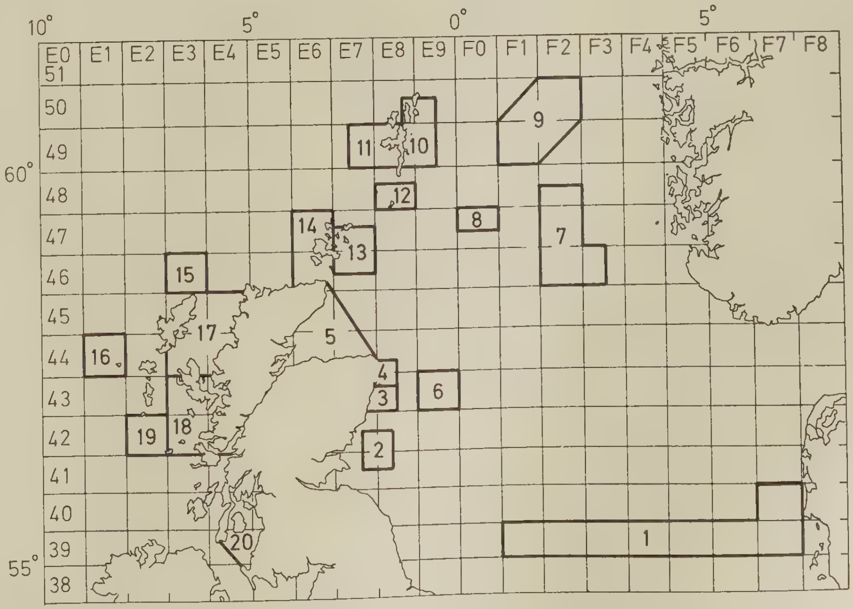
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Figure 2. Areas from which whiting were sampled for larval *Anisakis*: 1, Southern North Sea; 2, Arbroath; 3, Aberdeen; 4, Buchan; 5, Moray Firth; 6, Turbot Bank; 7, Ling Bank; 8, Bressay Shoal; 9, Bergen/Viking; 10, E. Shetland; 11, W. Shetland; 12, Fair Isle; 13, E. Orkney; 14, W. Orkney; 15, Butt of Lewis; 16, St. Kilda; 17, N. Minch; 18, S. Minch; 19, Barra; 20, Clyde.

few fish from research vessel catches were also examined.

The total length of all fish was recorded to the nearest cm below and the age of cod determined by otolith readings. It was not possible in the time available to obtain otolith readings for the whiting examined. Fish were then filleted so that the epaxial musculature was removed. In cod less than 40 cm in length this part of the musculature was examined for larval nematodes by candling over a strong light source. The musculature of larger cod was too thick to be examined in this way, so it was searched by slicing into thin strips. All whiting were examined by slicing. The hypaxial musculature (which surrounds the body-cavity) was searched by slicing in all fish. With practice larvae *in situ* may be accurately identified by eye. The number and locations of each species present in individual fish was recorded.

The relationship between the numbers of larval nematodes in the viscera and musculature of cod and whiting was determined by digesting individual fish from a sample using the pepsin–HCl digest method of Smith and Wootten (1975). Nematodes recovered were identified and counted. Fish used for digests had been dead for up to 36 h before examination.

Species of fish other than cod caught by research vessel in the areas shown in Figure 1 were examined for larval *Phocanema* by dissection or candling.

In this paper the terms prevalence and mean intensity of infection refer to the percentage of fish infected and the mean number of parasites per fish examined respectively.

Results

Geographical distribution

a) *Cod.* The abundance of larval *Phocanema* and *Anisakis* in cod fluctuated widely between different geographical areas around the Scottish coast.

Moray Firth. The total numbers of cod infected with *Phocanema* and with *Anisakis* were very similar but over 60% of larvae found were *Phocanema* (Table 1). Larval *Phocanema* was the more abundant in all age-groups except one year old fish; however, in one year old fish the level of infection with both nematode genera was low.

Ling Bank. Most larval nematodes found in cod of all age-groups at Ling Bank were *Anisakis* (Table 1). A few larval *Phocanema* occurred mainly in 3 year old and older fish.

Table 1. The prevalence and mean intensity of infection of cod from Scottish waters with larval *Phocanema* and *Anisakis* in 1971–73

Area and year	Age of cod in years	No. of cod examined	Cod with *Phocanema* Prevalence % cod infected	Infection mean No. larvae per cod	Maximum No. of larvae per cod	Cod with *Anisakis* Prevalence % cod infected	Infection mean No. larvae per cod	Maximum No. of larvae per cod
Moray Firth 1971–3....	1	157	3·1	<0·1	1	8·9	0·1	3
	2	368	14·4	0·3	29	17·9	0·3	6
	3	76	31·5	1·2	15	19·7	0·4	6
	$\geqslant 4$	12	58·3	1·8	5	25·0	0·7	3
Ling Bank 1971–3......	1	13	0	–	–	15·3	0·2	2
	2	192	<0·1	<0·1	1	41·6	0·8	8
	3	135	5·1	0·1	1	63·7	2·2	15
	4	70	1·4	<0·1	1	75·7	2·4	16
	5	46	8·6	0·1	4	63·0	2·8	19
	$\geqslant 6$	34	12·5	0·4	8	81·2	6·3	28
N. Coast 1971–3.......	1	56	33·9	0·6	8	5·4	0·1	2
	2	177	18·1	0·6	19	29·4	0·5	5
	3	93	39·8	1·7	27	20·4	0·4	14
	$\geqslant 4$	21	52·4	1·7	11	4·8	0·1	2
N. Minch 1973	2	59	45·8	1·9	18	47·5	0·9	5
	3	21	95·2	4·9	19	23·8	0·5	6
	$\geqslant 4$	16	68·8	7·6	64	25·0	0·3	1
S. Minch 1973.........	1 & 2	56	60·7	3·2	40	16·0	0·2	2
	$\geqslant 3$	29	75·9	4·9	31	10·3	0·1	2
Clyde 1971–2..........	1	68	2·9	<0·1	1	0	–	–
	2	83	20·5	0·8	30	0	–	–
	3	46	56·5	2·0	11	0	–	–
	$\geqslant 4$	15	73·3	5·7	15	0	–	–

North coast. Both larval *Phocanema* and *Anisakis* occurred commonly in cod from this area (Table 1). The prevalence of infection of cod with larval *Phocanema* was slightly higher than with larval *Anisakis*; however, numerically, *Phocanema* was by far the most abundant nematode in all age-groups of fish.

North Minch. Cod from the North Minch were also very heavily infected with larval nematodes (Table 1). Larval *Phocanema* was far more abundant than *Anisakis* especially in fish aged 3 and over.

South Minch. Cod from the South Minch were also very heavily infected with larval nematodes (Table 1). Most larvae recovered were *Phocanema*.

Clyde. Only larval *Phocanema* was found in cod from the Clyde (Table 1). Fish aged 3 and over were heavily infected.

b) *Whiting*. The prevalence and intensity of infection in whiting of length 30–39 cm from different geographical areas with larval *Anisakis* is shown in Table 2. Whiting outside this length range were not examined in sufficient numbers to be used in this comparison. With the exception of fish from the southern North Sea (1), South Minch (18) and Clyde (20), the prevalence of infection with *Anisakis* was over 50% in all areas sampled and was especially high in offshore areas of the northern North Sea. The mean intensity of infection was also highest in the offshore northern North Sea reaching a level of 14·3 larvae per fish in the Bressay Shoal (8) and Viking Bank (9) areas.

Off the Scottish east coast the level of infection was much lower and fairly uniform from the Angus coast to the Moray Firth. In the Orkney–Fair Isle–Shetland area the intensity of infection was intermediate between offshore northern North Sea and Scottish east coast values. However, within this area the mean intensity of infection rose from south to north. The mean intensity of infection was very low in the southern North Sea.

In whiting from north of Lewis (15), North Minch (17) and southwest of Barra (19) the mean intensity of infection was similar to that in fish from the Scottish east coast. In fish from St Kilda (16) the mean intensity of infection was rather higher and comparable with that found at Shetland (10, 11). The mean intensity of infection in whiting from the South Minch (18) and especially the Clyde (20) was very low.

Infection, age and length of the host

a) *Cod*. The prevalence and mean intensity of infection with larval *Phocanema* and *Anisakis* in cod of different age groups and areas are shown in Table 1. In most areas there was a considerable increase in the level of infection with both nematode species in older cod. An exception to this trend was shown by fish from both the North and South Minch where the level of infection with larval *Anisakis* decreased with age.

Table 2. The prevalence and mean intensity of infection of whiting from Scottish waters with larval *Anisakis* in 1971–74 (Fish 30–39 cm in length). The numbered areas are located in Figure 2.

Area	No. of fish examined	No. of fish infected	Prevalence % fish infected	Total No. of larvae found	Infection mean No. of larvae per fish	Standard error	Max. No. of larvae per fish
1. S. North Sea..........	134	45	33·6	96	0·7	0·1	7
2. Arbroath.............	80	69	86·3	240	3·0	0·1	12
3. Aberdeen............	102	87	85·3	369	3·6	0·1	25
4. Buchan..............	43	37	86·0	154	3·6	0·2	20
5. Moray Firth..........	102	76	74·5	265	2·6	0·3	20
6. Turbot Bank..........	146	145	99·3	1 356	9·3	0·2	32
7. Ling Bank............	120	114	95·0	1 014	8·5	0·3	55
8. Bressay Shoal.........	64	60	93·8	916	14·3	1·7	60
9. Bergen/Viking........	96	95	99·0	1 370	14·3	1·6	95
10. E. Shetland...........	123	97	78·9	740	6·0	0·2	38
11. W. Shetland..........	138	116	84·1	912	6·6	0·2	40
12. Fair Isle..............	104	95	91·3	650	6·3	0·2	43
13. E. Orkney............	72	65	90·3	328	4·6	0·2	23
14. W. Orkney...........	110	91	82·7	508	4·6	0·2	24
15. Butt of Lewis.........	136	111	81·6	485	3·6	0·1	22
16. St. Kilda.............	78	73	93·6	521	6·7	0·3	43
17. N. Minch............	114	71	62·3	279	2·5	0·1	18
18. S. Minch.............	50	23	46·0	68	1·4	0·2	24
19. Barra................	60	44	73·3	162	2·7	0·2	22
20. Clyde................	53	1	1·9	1	<0·1	–	1

Table 3. The prevalence and mean intensity of infection of whiting of different length groups from Scottish waters with larval *Anisakis* (No. of fish examined in parentheses). The numbered areas are located in Figure 2.

Area	Prevalence (% infected) of infection of whiting by 2 cm length groups							Mean intensity (larvae per fish) of infection of whiting by 2 cm length groups						
	⩽29	30 to 31·9	32 to 33·9	34 to 35·9	36 to 37·9	38 to 38·9	⩾40	⩾29	30 to 31·9	32 to 33·9	34 to 35·9	36 to 37·9	38 to 39·9	⩾40
1. S. North Sea .	14·3 (14)	16·7 (24)	30·3 (33)	23·1 (39)	57·7 (26)	58·3 (12)	47·8 (23)	0·1	0·4	0·6	0·5	1·2	1·4	0·9
2. Arbroath	35·3 (17)	75·0 (20)	95·0 (20)	80·8 (26)	100·0 (9)	100·0 (5)	100·0 (2)	0·8	1·6	2·9	3·0	4·8	6·0	1·5
3. Aberdeen	24·0 (25)	71·4 (21)	89·5 (19)	77·3 (22)	90·0 (20)	100·0 (20)	100·0 (25)	0·4	2·0	2·1	2·1	6·0	6·2	5·9
4. Buchan	48·3 (29)	80·0 (20)	87·5 (8)	88·9 (9)	100·0 (3)	100·0 (3)	100·0 (1)	1·1	3·0	1·6	6·9	2·3	4·3	4·0
5. Moray Firth . .	28·6 (21)	45·0 (20)	76·2 (21)	66·7 (21)	95·0 (20)	90·0 (20)	100·0 (20)	0·4	0·7	2·0	3·2	2·9	4·2	6·8
6. Turbot Bank .	80·0 (20)	97·4 (38)	100·0 (36)	100·0 (29)	100·0 (21)	100·0 (22)	100·0 (11)	3·4	6·7	7·5	9·0	11·5	14·9	24·1
7. Ling Bank . . .	57·1 (7)	85·2 (27)	93·3 (30)	100·0 (23)	100·0 (19)	100·0 (21)	100·0 (34)	1·6	3·3	4·4	10·8	10·0	17·0	47·2
8. Bressay Shoal.	75·0 (8)	76·9 (13)	100·0 (17)	94·1 (17)	100·0 (5)	100·0 (12)	100·0 (34)	3·1	6·2	10·4	13·4	16·8	29·0	40·2
9. Bergen/Viking	100·0 (4)	90·0 (10)	100·0 (21)	100·0 (23)	100·0 (22)	100·0 (20)	100·0 (28)	3·5	3·9	13·2	9·0	16·0	24·7	50·3
10. E. Shetland . .	75·0 (4)	54·5 (22)	69·6 (23)	80·0 (30)	92·9 (28)	95·0 (20)	100·0 (28)	0·8	1·0	3·2	8·0	9·1	7·5	16·1
11. W. Shetland . .	31·3 (16)	47·1 (17)	70·0 (20)	84·6 (26)	94·9 (39)	97·2 (36)	100·0 (24)	0·4	1·1	3·0	4·6	7·0	12·3	20·0
12. Fair Isle	50·0 (20)	100·0 (20)	76·2 (21)	90·0 (20)	91·3 (23)	100·0 (20)	93·3 (15)	0·7	4·0	3·6	4·4	7·0	12·3	13·9
13. E. Orkney	–	85·0 (20)	85·0 (20)	100·0 (9)	100·0 (17)	83·3 (6)	92·3 (13)	–	2·5	4·8	6·2	5·5	3·8	5·5
14. W. Orkney . . .	27·3 (22)	60·0 (20)	80·0 (20)	91·3 (23)	81·0 (21)	96·2 (26)	100·0 (6)	0·3	1·8	2·4	6·3	5·0	6·8	20·2
15. Butt of Lewis .	–	62·5 (24)	75·9 (29)	83·3 (30)	96·4 (28)	88·0 (25)	–	–	1·2	2·4	3·7	4·5	6·0	–
16. St. Kilda	–	90·9 (11)	95·2 (21)	90·0 (20)	95·0 (20)	100·0 (6)	–	–	7·9	4·9	8·0	6·8	6·2	–
17. N. Minch	55·0 (20)	36·7 (30)	61·3 (30)	76·9 (26)	66·7 (15)	91·7 (12)	–	1·1	1·2	1·9	1·7	4·7	5·7	–
18. S. Minch	30·0 (20)	47·4 (19)	38·9 (18)	54·5 (11)	50·0 (2)	–	–	0·4	0·8	1·8	1·7	3·0	–	–
19. Barra	50·0 (1)	0·0 (1)	50·0 (2)	70·6 (17)	83·3 (18)	72·7 (22)	91·7 (36)	0·5	0·0	1·5	1·7	4·5	2·2	10·5

b) *Whiting*. The prevalence and mean intensity of infection of whiting of different length groups with *Anisakis* from areas sampled is shown in Table 3. In all areas the prevalence and intensity of infection increased with length of the host. Fish less than 30 cm in length were relatively lightly infected in all areas but in larger fish, over 40 cm in length, the mean intensity of infection rose to high levels, especially in the northern North Sea.

Site of infection

a) *Cod*. The location of larval *Phocanema* in the musculature of cod of different age-groups are shown in Table 4. Larval *Phocanema* was found commonly in both hypaxial and epaxial musculature whereas over 95% of the larval *Anisakis* were located hypaxially. In one-year old cod most larval *Phocanema* occurred in the epaxial musculature, although the

Table 4. The number of larval *Phocanema* in the hypaxial and epaxial musculature of cod (all sampling areas combined).

Age of cod in years	Number of *Phocanema* Hypaxial musculature	Epaxial musculature	χ^2
1	87	108	2·3
2	308	231	11·0***
3	424	131	154·7***
4	152	39	66·9***
⩾5	104	12	73·0***

Table 5. The association between larval *Phocanema* and *Anisakis* in cod of different ages from the Moray Firth, north coast of Scotland and the North Minch

Area	Age of cod in years	Numbers of cod infected				χ^2 (2 × 2 table)
		Both genera	*Phocanema* only	*Anisakis* only	Neither genera	
Moray Firth	1	2	3	12	140	2·78
	2	9	44	57	258	0·04
	3	6	25	12	45	0·00
North coast Scotland	1	0	19	3	34	0·42
	2	12	20	40	105	0·81
	3	4	33	15	41	2·76
	4	0	11	1	9	0·00
North Minch	2	18	9	10	22	6·02*
	3	7	24	2	4	0·02

difference was not significant. However, in older fish significantly more larval *Phocanema* were found in the hypaxial musculature.

In areas in which both larval *Phocanema* and *Anisakis* occurred in cod, both larvae were rarely found together in the musculature of the same fish (Table 5), i.e. most infections consisted of only 1 of the 2 larval nematode genera. There was no evidence of association either positive or negative between *Phocanema* and *Anisakis*, except in 2 year-old fish from the North Minch, and infection of fish with the two genera is independent.

b) *Whiting*. The location of larval *Anisakis* in the musculature of whiting of different length groups is shown in Table 6. The great majority of larval *Anisakis* were located within the hypaxial muscles surrounding the body-cavity. Of those larvae found within the epaxial musculature almost all occurred ventrally so that they were found at the edges of fillets removed from the fish. The distribution of larval *Anisakis* within the musculature of whiting was similar in all length groups of fish.

Table 6. The location of larval *Anisakis* within the musculature of whiting of different length groups from sampling areas 1, 11, 13, 14, 15 and 17 in Figure 2

Length of fish (cm)	No. of fish examined	Total No. of larvae found	No. and percentage of larvae			
			Hypaxial musculature		Epaxial musculature	
			No.	% total	No.	% total
⩽ 29	72	37	33	89·2	4	10·8
30	69	84	79	94·0	5	6·0
31	66	103	95	92·2	8	7·8
32	76	163	149	91·4	14	8·6
33	77	190	170	89·5	20	10·5
34	74	216	211	97·7	5	2·3
35	79	282	258	91·5	24	8·5
36	77	361	325	90·0	36	10·0
37	69	339	300	88·5	39	11·5
38	52	332	289	87·0	43	13·0
39	65	544	462	84·9	82	15·1
⩾ 40	66	685	635	92·7	50	7·3

Association between numbers of larval *Anisakis* in viscera and musculature

a) *Cod*. The musculature and viscera of 24 cod from the Ling Bank were examined for the presence of *Anisakis*. The mean number of larvae in the viscera was 23, much higher than the mean level of 3 larvae in the infected musculature. The correlation coefficient between the number of *Anisakis* in the viscera and in the musculature was 0·12 showing no evidence of association between the levels of infection of the two sites.

b) *Whiting*. The proportions of larval *Anisakis* found in the viscera and musculature of two samples of whiting from the Moray Firth and the Ling Bank are shown in Table 7. In both samples most of the *Anisakis* occurred in the musculature and in the Ling Bank sample this difference was statistically significant. There was a significant positive correlation between the numbers of larvae in the viscera and musculature of both samples (Moray Firth, $r = 0{\cdot}55$; Ling Bank, $r = 0{\cdot}59$).

Occurrence of larval *Phocanema* in fish other than cod

Of 10 fish species caught in the cod sampling area, examination revealed larval *Phocanema* in 5, namely long rough dab, dragonet, witch, haddock and poor cod in at least one of the areas sampled (Table 8). Only long rough dab was infected in all areas. The prevalence of infection in all fish species was low, and only one or two larvae were found per infected fish. The larvae of *Phocanema* were found only within the musculature.

Table 7. The distribution of larval *Anisakis* between the viscera and musculature of whiting

	Viscera	Musculature	χ^2
Moray Firth (90 fish)			
Total No. larvae..........	324	355	1·54
Mean No. larvae per fish...	3·6	3·9	
% Total No. larvae........	47·7	52·3	
Ling Bank (50 fish)			
Total No. larvae..........	889	1 376	104·7***
Mean No. larvae per fish...	17·8	27·5	
% Total No. larvae........	39·2	60·8	

Table 8. The prevalence of larval *Phocanema* in fish other than cod from Scottish waters during 1971–73

Area	Fish species	Number examined	Length range in cm	Number infected	% infected
Moray Firth	Long Rough Dab (*Hippoglossoides platessoides*)	117	12–23	7	6·0
	Dragonet (*Callionymus lyra*)	35	11–24	6	17·1
	Common Dab (*Limanda limanda*)	244	9–23	0	–
	Lemon Sole (*Microstomus kitt*)	139	11–28	0	–
	Norway Pout (*Trisopterus esmarkii*)	34	9–15	0	–
	Poor Cod (*Trisopterus minutus*)	125	9–20	0	–
	Whiting	217	6–20	0	–
	Haddock	134	12–28	0	–
North coast Scotland	Norway Pout	48	9–17	0	–
	Poor Cod	95	10–22	0	–
	Whiting	55	11–26	0	–
	Haddock	24	13–24	0	–
North Minch	Long Rough Dab	95	5–19	8	8·4
	Witch (*Glyptocephalus cynoglossus*)	57	14–29	0	–
	Poor Cod	69	7–17	0	–
South Minch	Long Rough Dab	684	2–25	62	9·1
	Dragonet	53	5–18	3	5·7
	Witch	95	9–39	8	8·4
	Poor Cod	158	8–23	5	3·2
	Haddock	16	15–25	1	6·3
	Lemon Sole	14	13–31	0	–
	Norway Pout	100	11–15	0	–
	Megrim (*Lepidorhombus whiffiagonis*)	12	7–42	0	–
Clyde	Long Rough Dab	236	9–20	7	2·3
	Dragonet	8	8–11	0	–
	Norway Pout	124	7–16	0	–

Discussion

The larvae of *Phocanema* and *Anisakis* were widespread in cod and whiting from Scottish waters but the abundance of the two genera varied considerably between geographical areas. Young (1972) found similar variations in the abundance of larval *Phocanema* and *Anisakis* in cod from different areas around the British Isles and related this to the distribution of the mammalian final hosts.

The significance of variations in the distribution of the invertebrate intermediate hosts of *Phocanema* and *Anisakis* on the occurrence of larvae in fish from different areas in poorly known. Work in progress suggests that the prevalence of larval *Anisakis* in euphausiid intermediate hosts in Scottish waters may be highest in the central northern North Sea where these crustaceans appear to be most abundant (J. W. Smith, personal communication).

The abundance of larval nematodes in the musculature of cod from Scottish waters has increased dramatically since 1958 (Rae, 1963; 1972). It is impossible to determine with certainty if both *Phocanema* and *Anisakis* or only one of these genera has been responsible but as both genera rarely occur together in the musculature of an individual cod an increase in the abundance of only one genus could lead to an increase in the overall level of larval nematode infection. Northern North Sea cod are heavily infected with larval *Anisakis* and it seems reasonable to suggest that this genus is largely responsible for the observed increase in infection of cod from this area. This is also suggested by the remarkable increase in abundance of *Anisakis* in whiting. In 1960–63 over 14 500 whiting from Scottish waters, including over 9000 from the northern North Sea, were examined at the Marine Laboratory for the presence of larval nematodes within the musculature. The prevalence of infection was less than 1·5% in fish from all areas which contrasts dramatically with the levels found in 1971–74.

In some areas such as the Moray Firth, north coast and the North Minch either or both *Phocanema* and *Anisakis* may be responsible for observed increases in nematode abundance whilst in other regions like the South Minch and Clyde *Phocanema* alone is probably involved.

Apparent increases in the abundance of both *Phocanema* and *Anisakis* in cod and whiting are probably due to changes in the abundance or population structure of one or more of the host species but no clear-cut explanation is possible at the present time.

Accumulation of larval nematodes with increasing age and length of cod and whiting probably occurs not only because each larva is apparently long-lived but also because larvae are continually acquired by most fish throughout their lives. In addition, larger and older fish consume greater quantities of food which will probably result in larger numbers of larval nematodes being ingested. Infections of fish may arise through the ingestion of the invertebrate intermediate host or already infected prey fish. The latter infection route may be particularly important in cod of the size examined in this study which feed primarily on fish or larger invertebrates (Rae, 1967). Commercial sized whiting also feed heavily on fish, especially small gadoids (Jones, 1954). Experimental transfer of larval *Anisakis* from fish to fish was achieved by Smith (1974) and Wootten and Smith (1975) whilst transfer of *Phocanema* from cod to cod was accomplished by Scott (1954).

Several of those fish species found infected with *Phocanema*, including the long rough dab, dragonet and witch, are known to form part of the diet of cod in Scottish waters (Rae, 1967). Larval *Anisakis* are found in numerous fish species so cod and whiting may acquire this parasite from many different prey fish. The apparent almost total absence of larval *Phocanema* in whiting, only eight infected specimens were found, may also be due to dietary differences between this host and the cod.

A similar distribution of larval nematodes within the musculature of cod to that found in the present study was recorded by Rae (1963), Young (1972) and Platt (1975). In whiting a rather larger proportion of the total numbers of larval *Anisakis* occurred in the epaxial muscles compared with cod. The proportion of larvae was similar to that found in the epaxial muscles of herring by Smith and Wootten (1975). Larval *Anisakis* can presumably penetrate relatively further into the musculature of smaller fish such as whiting and herring compared with the larger cod. A similar mechanism might account for the higher proportion of *Phocanema* in the epaxial musculature of one year old cod compared with older fish (Young 1972; Platt 1975).

The relative distribution of larval *Phocanema* and *Anisakis* between the viscera and musculature of cod was similar to that recorded by Young (1972) and Platt (1975). In whiting however the proportion of larval *Anisakis* in the musculature was much higher, even exceeding that recorded in herring (Smith and Wootten, 1975). These authors found a considerable migration of larval *Anisakis* from the viscera into the musculature after death of the host; a similar migration may occur in cod and whiting. As the fish used in the present study to measure visceral burdens had been dead up to 36 hours before examination it may be that the proportion of larvae found in the musculature was higher than occurred in life.

The significant positive correlation found between the numbers of larval *Anisakis* in the viscera and musculature of whiting compares with the similar association found in herring (Smith and Wootten, 1975).

That both larval *Phocanema* and *Anisakis* rarely occurred together in the musculature of individual cod is difficult to explain, especially since information on the visceral larval nematode burdens of each fish was not available. Differences in the feeding habits of individual cod probably provide an explanation.

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Effects of climatic cycles on the relative abundance and availability of commercial marine and estuarine species

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Fluctuations in the total weight and number of species, and the volume of each of 24 species in the annual catch of marine and estuarine fisheries of the Maine coast, representing 80% of total production, are highly significantly correlated with sea temperature cycles. Another seven species representing an additional two percent of total annual catch are significantly correlated in relative abundance or availability with the same cycles.

Introduction

Fluctuations in the number and abundance of commercial marine species, although usually associated with latitude, also occur during climatic cycles. Examples of these relationships are characteristic of the northern Gulf of Maine, normally the habitat of boreal species but during years of relatively high sea temperature intruded by vertebrates from the south in sufficient numbers to become commercially important. Abrupt and spectacular increases in the abundance of resident warm water invertebrates that have persisted as relict populations in a few isolated anomalous areas also occur. Conversely, during periods of low sea temperature those species whose southern range terminus is the Gulf of Maine increase rapidly in abundance and replace in economic importance those species at or near the northern end of their range.

Materials

Sea surface temperature has been recorded three times daily or more frequently at Boothbay Harbor, Maine, since 1905 by either the National Marine Fisheries Service or the Maine Department of Marine Resources (Welch, 1976) and indicates that periodic mean annual highs and lows occur at approximately decade intervals (Figure 1 and Table 2). Of particular significance and interest is the 29 year subcycle 1939–1967 in which the second coldest and the warmest years of record occurred.

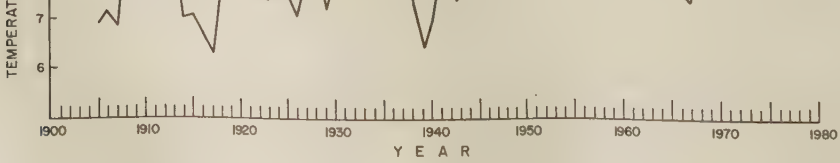

Figure 1. Sea surface temperature, Boothbay Harbor, Maine (as measured by the National Marine Fisheries Service and the Department of Marine Resources) 1905–1975.

Maine Landings is the official National Marine Fisheries Service publication of species volumes and values taken in the commercial fisheries of the state. More than 50 species have been listed in the period since 1939.

Methods

Simple linear correlation utilizing arithmetic means of sea surface temperature at Boothbay Habor, Maine, have been used throughout present studies. All catch data are annual totals in metric tons.

Results

Associated with the 1939–1967 temperature period were major fluctuations in total volume, the number of species caught, and the relative abundance or availability of each species in the commercial marine and estuarine fisheries of the northern Gulf of Maine.

There is a highly significant correlation of 0·59 ($r_{0 \cdot 01} = 0 \cdot 47$) between mean annual sea surface temperature, as measured at Boothbay Harbor, and the total number of species represented in each annual catch. Mean annual sea surface temperature in 1939 was 6·4°C and the number of species reported was 30. By 1949 the annual mean temperature had increased to 10·1°C and the number of species to 41. Following an apparent above optimum five-year peak mean of 10·4°C from 1951 to 1955, during which the average number of species reported was 38, temperature declined to 7·3°C in 1967, and by 1971 the number of species had decreased to 35. In 1974, temperature had risen to an annual mean of 9·2°C and the species had increased to 46, several of which do not reach legal or commercial size for 3 to 8 years after spawning. Although more species were caught during high temperature years than during cold periods, both extremes were associated with the commercial extinction of several previously important species.

In addition to fluctuations in the total number of species and the total volume of the annual catch, the magnitude of the catch of each species has fluctuated markedly with sea temperature cycles. Highly significant correlation coefficients between mean annual sea temperature as measured at Boothbay Harbor and the catch of 24 individual species range from 0·86 for lobster (*Homarus americanus*) to −0·91 for sea scallop (*Placopecten magellanicus*) (Tables 1 and 2). The 24 species are equally divided between inverse and positive correlations. Of the seven species having correlation coefficients between catch and sea temperature significant at the 5% level, only one, the sea urchin (*Strongylocentrotus droebachiensis*) is inversely correlated (Table 4).

Between 1939 and 1967 more than 3 million metric tons of fish, shellfish, and other commercially important marine organisms were landed at Maine ports. A highly significant coefficient of correlation ($r = 0 \cdot 63$, $r_{0 \cdot 01} = 0 \cdot 470$) between mean annual sea surface temperature and total annual catch indicates that sea temperature is probably the principal factor influencing volume, since neither changes in fishing effort nor market conditions were adequate to account for the magnitude of annual fluctuations in volume (Anon, 1939–1971).

Increased food requirements and improved market conditions as a result of World War II were of major significance in stimulating greater fishing effort. Fish were increasingly in demand as substitutes for Office of Price Administration regulated meats, and stocks were obviously adequate to allow a rapid increase in the catch of all cold water species such as cod (*Gadus morhua*), hake (*Urophycis tenuis*), rock

Table 1. Scientific names of species listed in Tables 2, 3, and 4

Table 2 species	
Lobster	*Homarus americanus*
Gray Sole	*Glyptocephalus cynoglossus*
Menhaden	*Brevoortia tyrannus*
Pollock	*Pollachius virens*
Alewife	*Alosa pseudoharengus*
Herring	*Clupea harengus*
Winter Flounder	*Pseudopleuronectes americanus*
Squid	*Loligo pealii*
Smelt	*Osmerus mordax*
Mussel	*Mytilus edulis*
Shrimp	*Pandalus borealis*
Scallop	*Placopecten magellanicus*
Table 3 species	
Oyster	*Crassostrea virginica*
Hard Clam	*Mercenaria mercenaria*
Dab	*Hippoglossoides platessoides*
Cusk	*Brosme brosme*
Cod	*Gadus morhua*
Hake	*Urophycis tenuis*
Rock Crab	*Cancer irroratus*
Bloodworm	*Glycera dibranchiata*
Soft Clam	*Mya arenaria*
Sandworm	*Nereis virens*
Salmon	*Salmo salar*
Periwinkle	*Littorina littorea*
Table 4 species	
Haddock	*Melanogrammus aeglefinus*
Butterfish	*Poronotus triacanthus*
Wolffish	*Anarhichas lupus*
Yellowtail	*Limanda ferruginea*
Whiting	*Merluccius bilinearis*
Halibut	*Hippoglossus hippoglossus*
Sea Urchin	*Strongylocentrotus droebachiensis*

Table 2. Correlation coefficients between sea temperature and total number of species and total volume of catch in the commercial marine and estuarine fisheries in the northern Gulf of Maine. The correlation coefficients for the catch of 12 individual species are also given ($r_{0.01} = 0{\cdot}47$)

Year	Sea surface temperature (°C)	Total number of species	Total catch (thousands of metric tons)	Lobster (hundreds of metric tons) 5–6–7 years later	Gray sole (metric tons) same year	Menhaden (metric tons) same year	Pollock (hundreds of metric tons) same year	Alewife (hundreds of metric tons) 4 years later	Herring (thousands of metric tons) 2 and 3 years later	Winter flounder (metric tons) same year	Squid (metric tons) same year	Smelt (metric tons) 2 and 3 years later	Mussel (metric tons) 6 years later	Shrimp (log of metric tons) 4 years later	Scallop (metric tons) 7 and 8 years later
1939..	6·4	30	30	79	378	0	11	8	31	276	0	229	1 240	2·12	146
1940..	7·0	34	67	85	331	0	16	4	27	132	0	294	1 050	2·25	218
1941..	7·8	33	73	80	269	0	9	6	29	112	0	284	18	2·40	219
1942..	8·1	36	76	81	357	0	12	6	34	145	0	263	56	1·86	232
1943..	7·4	35	61	81	356	0	10	7	36	395	0	210	175	1·95	202
1944..	8·0	36	73	88	341	38	12	8	46	664	0	116	147	1·08	157
1945..	8·4	36	84	89	362	0	26	15	69	212	0	64	203	0·70	126
1946..	8·5	40	87	95	428	6	30	14	76	489	0·3	57	130	0·48	88
1947..	9·2	40	100	97	280	11	20	16	76	275	0·2	55	23	1·30	82
1948..	8·2	39	138	101	342	2 280	29	13	56	395	0	50	37	1·67	124
1949..	10·1	41	133	98	345	222	26	11	47	378	9·0	49	47	1·23	80
1950..	9·6	41	160	102	548	687	28	15	56	722	10·0	53	55	0	80
1951..	10·8	40	100	100	742	274	24	17	51	1 026	2·0	57	18	0	49
1952..	10·1	38	134	103	620	991	29	21	51	639	0·5	65	55	0	41
1953..	11·1	39	110	102	725	2 665	23	18	55	460	2·0	57	11	0	48
1954..	10·2	38	129	102	577	1 822	19	14	67	540	0·8	38	23	0·30	67
1955..	10·0	37	116	101	536	552	23	7	74	417	3·0	46	1	0·70	75
1956..	9·2	39	126	99	541	124	23	6	66	228	0·7	46	3	1·61	93
1957..	9·4	38	133	100	538	0	17	8	61	315	1·0	31	9	1·46	121
1958..	8·5	39	144	95	457	0	20	8	47	211	3·0	33	7	2·19	129
1959..	8·3	39	121	91	361	16	17	7	48	155	0	41	14	2·38	108
1960..	8·9	40	134	84	367	0	18	7	70	165	0	56	109	2·61	183
1961..	8·5	40	90	86	258	0	18	14	48	72	0	75	168	2·97	219
1962..	8·1	40	134	86	271	0	12	8	30	33	0·2	87	177	3·22	163
1963..	8·8	40	130	88	323	0	11	7	29	22	3·0	103	160	3·48	197
1964..	8·3	39	87	84	226	0	6	10	28	34	0	94	137	3·75	335
1965..	7·7	39	93	79	224	0	5	8	31	31	0	56	68	4·05	402
1966..	7·6	37	91	77	188	0	5	7	29	42	0	46	127	3·91	283
1967..	7·3	38	90	75	240	0	5	9	21	47	0	45	199	3·90	463
$r =$		0·59	0·63	0·86	0·75	0·64	0·63	0·62	0·60	0·57	0·48	−0·57	−0·59	−0·66	−0·91

crab (*Cancer irroratus*), soft shell clams (*Mya arenaria*), smelts (*Osmerus mordax*), mussels (*Mytilus edulis*), shrimp (*Pandalus borealis*), scallops, and periwinkles (*Littorina littorea*). The crab catch decreased more than 50% during the 1943–1948 period as the result of the loss of a major cannery market; therefore, these years have been omitted from the study. The influence of economic conditions was especially evident in the lobster fishery, although the magnitude of the lobster population has been shown to be temperature dependent (Dow, 1969). In other fisheries representing 60% of total catch, increases came well after World War II. The 12 species listed in Table 2 are the only species highly significantly correlated with sea temperature for which catch records are complete for the entire 1939–1967 period.

The lobster fishery, greatly curtailed during the economic depression of the 1920's and 1930's, was expanded by area and in season and the result of this expansion was an increase of nearly 200% in the catch by 1945. With optimum or nearly optimum sea temperatures in the 1950's, the annual catch increased nearly 300%.

Discussion

How sea temperature influences abundance varies with species. As the Gulf of Maine is, except for the

Table 3. Correlation coefficients between sea temperature and catch of 12 individual species

Year	Sea surface temp. (°C)	Oyster (metric tons) 3 years later	Hard clam (metric tons) same year	Dab (metric tons) same year	Cusk (metric tons) same year	Cod (metric tons) same year	Hake (metric tons) same year	Rock Crab (metric tons) same year	Bloodworms (metric tons) 3-year-olds	Soft Clam (thousands of metric tons) 5 years later	Sandworms (metric tons) 3-year-olds	Salmon (metric tons) same year	Periwinkle (metric tons) same year
1938......	7·3	–	–	–	–	–	–	–	–	–	.	7·1	–
1939......	6·4	–	0	–	–	3 345	2 140	508	–	–	–	3·4	–
1940......	7·0	–	2	173	–	2 506	2 298	412	–	2·6	–	9·3	22
1941......	7·8	–	54	288	–	1 978	2 154	759	–	4·5	–	1·2	11
1942......	8·1	–	56	273	269	2 096	2 962	581	–	3·6	–	1·4	27
1943......	7·4	–	36	193	169	2 985	3 498	–	–	4·1	–	0·01	21
1944......	8·0	–	14	229	173	2 136	2 720	–	–	3·9	–	3·4	20
1945......	8·4	–	137	239	176	2 698	2 520	–	–	3·1	–	3·8	23
1946......	8·5	–	76	249	333	3 019	3 070	–	–	2·3	–	0·5	9
1947......	9·2	–	44	173	257	1 907	1 585	–	–	2·5	–	1·6	18
1948......	8·2	–	131	256	460	2 897	2 528	–	–	1·9	–	0	9
1949......	10·1	–	268	266	546	2 388	2 035	333	95	1·7	71	0·5	5
1950......	9·6	–	228	732	636	2 602	2 237	651	115	1·2	111	0·3	1
1951......	10·8	2·6	258	916	557	2 099	1 428	340	109	1·1	129	0·7	1
1952......	10·1	1·4	192	847	493	1 844	1 802	170	92	0·9	81	0	2
1953......	11·1	2·0	152	641	415	1 489	1 725	271	77	0·7	128	0	5
1954......	10·2	2·6	132	750	328	1 475	1 440	236	108	0·7	132	0	3
1955......	10·0	1·5	113	629	274	1 119	1 088	226	140	0·9	122	0	4
1956......	9·2	1·6	131	657	181	1 071	1 304	544	194	0·8	244	0	12
1957......	9·4	1·2	164	523	237	922	1 158	343	249	0·9	278	0	9
1958......	8·5	1·3	115	439	246	–	–	549	270	0·8	292	–	14
1959......	8·3	0·4	73	395	270	–	–	616	264	0·8	307	–	16
1960......	8·9	0·8	29	323	262	–	–	556	249	0·9	369	–	15
1961......	8·5	0·7	6	312	272	–	–	716	258	1·4	350	–	15
1962......	8·1	0·4	1	234	276	–	–	794	241	1·4	325	–	16
1963......	8·8	1·9	–	206	213	–	–	912	205	1·5	361	–	16
1964......	8·3	1·8	–	260	168	–	–	891	223	1·9	320	–	22
1965......	7·7	0·2	–	345	130	–	–	838	189	2·3	316	–	23
1966......	7·6	0	–	395	137	–	–	805	177	2·3	305	–	23
1967......	7·3	0	–	342	88	–	–	761	159	3·0	304	–	25
$r =$		0·82	0·80	0·74	0·70	−0·61	−0·63	−0·63	−0·67	−0·66	−0·81	−0·84	−0·86
$r_{0.01}$		0·61	0·52	0·48	0·50	0·58	0·58	0·53	0·58	0·48	0·58	0·56	0·48

anomalous Gulf of St. Lawrence, at the northern limit of range of the hard clam (*Mercenaria mercenaria*) and the oyster (*Crassostrea virginica*), the only period when these two species are relatively abundant is when the temperature is high enough to permit successful spawning and progeny survival. During cold periods a nucleus of subtidal survivors continues in deeper water where token spawning occurs infrequently and old age is commonplace. Some specimens of each species may reach an age of 25 years or more, and the interval between commercially important progeny survival may be in excess of twenty years. Oysters in the Sheepscot River were not commercially abundant after the 1908–1910 year classes had been harvested until the high temperature period from 1947 to 1960 when the fishery was revived. Sampling of the population in 1954 identified relict survivors from the 1931–1933 and 1937 year classes when mean annual sea temperatures were relatively high, 8·6 to 9·1°C (Taxiarchis et al, 1954).

The hard clam resource had been commercially exhausted by 1937 when the first of three important year classes resupplied the fishery. The 1947 and 1952 year classes extended the life of the fishery to 1962; in recent years an increase in sea temperature to an annual mean of 9·4°C has resulted in a modest recovery of the stock and a resumption of the fishery (Anon, 1975).

With the exception of the American lobster and the soft shell clam, catches made by Maine fishermen reflect relative abundance and availability rather than absolute abundance. Results of sea-temperature-species abundance studies were initially reported for the lobster in Canada in 1953 (Martin, 1953) and in Maine in 1956 (Dow and Trott, 1956), although interest in temperature-abundance relations had been

Table 4. Correlation coefficients between sea temperature and catch of 7 individual species (r values for all are 0·37 at 0·05)

Year	Sea surface temp. (°C)	Haddock (metric tons) 4 years later	Butterfish (metric tons) same year	Wolffish (metric tons) same year	Yellowtail (metric tons) same year	Whiting (hundreds of metric tons) 4 years later	Halibut (metric tons) same year	Sea urchin (metric tons) same year
1939.........	6·4	805	0	19	0	9	11	24·7
1940.........	7·0	814	0	31	0	17	16	47·6
1941.........	7·8	1 001	0	37	0	24	13	46·6
1942.........	8·1	1 203	0	36	0	20	8	30·4
1943.........	7·4	1 537	0	92	0	26	10	24·8
1944.........	8·0	2 745	0	91	14	39	4	35·7
1945.........	8·4	2 865	0	88	45	56	5	29·4
1946.........	8·5	2 965	0·01	78	24	70	9	10·5
1947.........	9·2	2 110	0	54	41	88	18	26·2
1948.........	8·2	2 440	0	98	53	105	19	81·7
1949.........	10·1	2 157	0·1	72	54	57	20	36·1
1950.........	9·6	2 216	19·2	97	66	42	34	15·4
1951.........	10·8	1 819	1·8	89	37	114	45	25·0
1952.........	10·1	1 968	5·7	74	25	67	35	32·6
1953.........	11·1	1 858	8·0	63	26	72	31	13·4
1954.........	10·2	1 813	8·9	59	11	107	42	24·7
1955.........	10·0	1 544	80·5	50	14	106	61	26·5
1956.........	9·2	1 739	61·0	44	24	50	42	53·8
1957.........	9·4	1 334	17·5	63	18	64	56	45·7
1958.........	8·5	1 154	125·1	46	29	81	62	28·9
1959.........	8·3	1 305	21·3	47	51	72	44	49·0
1960.........	8·9	1 337	6·2	39	30	115	41	50·2
1961.........	8·5	853	3·3	22	30	126	31	33·6
1962.........	8·1	804	2·1	20	8	135	42	33·4
1963.........	8·8	1 066	6·0	22	0	94	42	38·3
1964.........	8·3	812	2·7	12	3	131	35	54·8
1965.........	7·7	446	0·7	19	3	81	42	57·2
1966.........	7·6	459	0	5	10	67	46	64·9
1967.........	7·3	372	0	7	35	45	45	50·2
$r =$		0·45	0·42	0·42	0·42	0·41	0·37	−0·38

stimulated by research in the 1949–1954 period on abundance fluctuations in the isolated inshore sea scallop populations of the Maine coast (Dow, 1962) and by studies elsewhere in New England (Taylor et al, 1957).

Four to seven years after hatching nearly all lobsters will be recruited to the fishery by moulting during the summer-fall months from sublegal to legal size. The magnitude of the recruited supply appears to depend upon the effect of sea temperature on feeding activity and growth as well as upon survival of juveniles during the first year. The correlation coefficient between annual mean sea temperature and lobster catch 5, 6, and 7 years later, based on 29 observations, is 0·86, ($r_{0·01} = 0·47$).

Scallop survival to commercial size appears to be limited by sea temperature both before and after the August–October spawning period. Good survival through the larval and early juvenile stages usually results in commercially important crops six to nine years later, which will contribute 65 to 95% of the annual catch (Dow and Baird, 1960).

Commercial size soft clam abundance at median age of five years is limited by green crab (*Carcinus maenas*) and other predators which increase during high temperature years (Dow, 1972). Although the growing season of clams is prolonged when sea temperature is near the upper limit of the northern Gulf of Maine, survival because of increased predation declines drastically.

Of the important commercial species, the circumpolar northern shrimp, four years of age at commercial size, appears to have the lowest temperature tolerance and has the Gulf of Maine as the southern limit of its range in the northwest Atlantic (Wigley, 1960).

Sea temperature influence on abundance is especially apparent with those species whose monetary value induces intensive fishing effort by which changes in abundance become more evident: lobster, soft clam, hard clam, scallop, shrimp, oyster, bloodworm (*Glycera dibranchiata*), sandworm (*Nereis virens*), herring (*Clupea harengus*), flounders (*Glyptocephalus cynoglossus*, *Pseudopleuronectes americanus*, and *Hippoglossoides platessoides*), rock crab, and the rainbow smelt.

Some species not listed in *Maine Landings* are caught incidental to other fisheries during the lower temperature years and include the shrimps (*Pandalus montagui*, *Crago septemspinosus*, and *Pandalus propinquuis*) (Apollonio and Dunton, 1969). During the high temperature years several warmer water species are caught but may not be reported by species. These include, among others, the round herring (*Etrumeus sadina*), the billfish or saury (*Scomberesox saurus*), tautog (*Tautoga onitis*), bluefish (*Pomatomus saltatrix*), fluke (*Paralichthys dentatus*), surf clam (*Spisula solidissima*), and the razor clam (*Ensis directus*).

Market acceptability restricts rock crab carapace width to about 90 mm or greater, although there is no legal minimum size. This restriction means that each year's catch will consist of three or more year classes comparable to the year class composition of the lobster catch. Thus, the magnitude of both lobster and crab catches will depend upon sea temperature prior to their most recent moult.

The availability of wolffish (*Anarhichas lupus*), halibut (*Hippoglossus hippoglossus*), whiting (*Merluccius bilinearis*), sea herring, cod, and hake appears to have been reduced appreciably in recent years by intensive offshore fishing by foreign vessels. Landings of both cod and hake after 1957 have been excluded from this study for that reason.

The majority return of river herring (*Alosa pseudoharengus*) to spawning areas where they are caught occurs in the fourth year of age, while the anadromous rainbow smelt catch consists largely of two- and three-year-old fish (Flagg, 1972). Bait worms at acceptable commercial size are three years of age (Creaser, 1973) and the median age of mussels in the commercial catch is six years.

The commercially marginal common squid (*Loligo pealii* Lasueur) occurs abundantly in the northern Gulf of Maine only during high temperature periods. No catches were reported during the low temperature years 1939–1945; 82% of all squid catches occurred during years when the annual sea temperature at Boothbay Harbor was 9·2°C or higher.

The bivalve marine wood borer (*Xylophaga atlantica*) is evident only during high temperature years. In 1974 and 1975 it reappeared for the first time since the 1949–1955 period when it was very destructive to lobster traps and other wood structures (Dow and Baird, 1953).

Some species which are not intentionally fished in the Gulf of Maine (for example, the blue crab, *Callinectes sapidus*) are so rarely caught that their infrequent and incidental capture in lobster traps during only very warm years is of great interest to both fishermen and scientists. Such captures are generally reported at the time.

Conclusions

1. On the basis of the evidence, sea temperature of the Gulf of Maine has been the principal environmental regulator of species abundance and availability.

2. Dependence on periodic and widely varying sea temperature cycles for maximum abundance of each of more than 30 commercially important species creates major problems to effective fisheries management.

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Classification of sea water in terms of quanta irradiance

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From a large body of data of quanta irradiance (350–700 nm) in different water masses the depth has been derived at which the percentage of surface irradiance of quanta is 30%, 10%, 3%, and 1% respectively. It has been shown that the relationship between the 10% level and the other levels can be expressed by simple equations with an accuracy sufficient for most practical purposes. Thus three of the levels can be computed if one is known. This implies that a classification of sea water in terms of transmittance of quanta irradiance is established for the whole euphotic zone.

Introduction

Quanta meters were introduced primarily for the purpose of measuring the number of quanta within the wavelength range 350–700 nm available for photosynthesis at different levels in the sea. The experimental material collected with the use of the Danish and French quanta meters (Jerlov, 1976) is now comprehensive and fairly representative of different water masses. It seems therefore opportune to investigate the possibility of bringing about some systematic order into the volume of data.

The existing optical classification in terms of spectral transmittance of downward irradiance (Jerlov, 1976) comprises five types of ocean surface water (0–10 m). A special classification applies to coastal waters of Scandinavia and western North Atlantic. Very turbid waters are not included. Both classifications, resting on a solid basis of observations, have proved their usefulness in the practical work; but they have so far been extended to greater depths for blue light only.

It is obvious that the transmittance of quanta through the uppermost layer (0–10 m) can readily be computed from spectral transmittance data for the optical water types. It may be rewarding, however, to make a direct attempt of arranging the experimental quanta data in categories representing the whole photic zone.

Experimental material

Quanta observations have been made in many of water masses of different transparency from the

Table 1. Stations where quanta observations have been made

Notation	Region	No. of observations	Reference
1.	Danish waters	37	Højerslev (1974)
2.	North Sea	101	Højerslev (personal communication)
3.	Off West Africa	16	Kullenberg (personal communication)
4.	Off West Africa	22	Morel and Calouménos (1973)
5.	Off Iceland	1	Højerslev and Lundgren (in press)
6.	California Bay	9	Nygård (1968)
7.	West Mediterranean	11	Højerslev (1974)
8.	Off Equador, Panama	11	Nygård (1973)
9.	Off Equador, Panama	11	Morel (1973)
10.	Drake Passage	3	Kullenberg (personal communication)
11.	Carribean Sea	7	Nygård (1973)
12.	Carribean Sea	7	Morel (1973)
13.	Sargasso Sea	1	Nygård (1973)
14.	Sargasso Sea	4	Morel (1973)

clear Sargasso Sea to the productive region off West Africa (Table 1). Of particular interest are the "Discoverer" measurements in waters off Equador, Panama, in the Carribean and the Sargasso Sea which allow of a direct comparison between observations obtained with the Danish (Jerlov and Nygård, 1969b) and with the French (Prieur, 1970) quanta meter. The considerable number of data obtained in the North Sea originate from the limited area of the Fladen Ground during August 1975 and June 1976. Danish waters i.e. the Baltic, the Sound, the Belts, the Kattegat and the Skagerrak are not dealt with separately even if they contain an abundance of yellow substance.

Data have been collected under a variety of weather conditions. Those which are palpably erroneous have of course been omitted. Observations with a low sun (<10°) have not been used since their accuracy is severely affected by a rapid change of daylight and of reflectance at the surface.

Representation of data

Some examples of depth profiles of downward quanta irradiance (log values) are presented in Figure 1. A typical feature is the fast decrease in the surface stratum due to absorption of the longwave light and in turbid water also due to that of shortwave light. Another marked curvature appears round 50 m in clear water, identical with that for blue light. It gradually disappears when the water becomes more turbid and the profile below the surface layer is transformed into an almost straight line. The narrowing with increasing depth of the originally broad wavelength band from 350 to 700 nm proceeds until at the lower end of the photic zone most quanta are carried by wavelengths that have maximum transmittance.

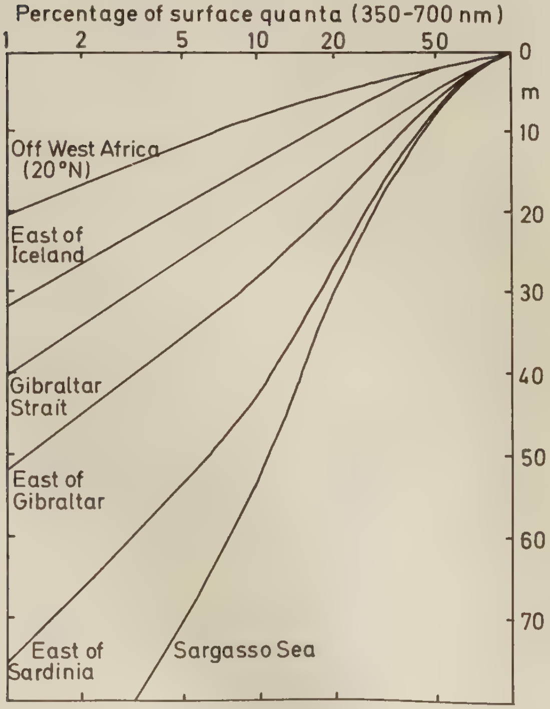

Figure 1. Depth profiles of quanta irradiance (350–700 nm) as percent of surface value.

With a view to the biological interest in quanta measurements we shall, as an initial approach, consider the depths where the percentage of surface quanta is 30%, 10%, 3% and 1%, respectively. Such a four-point representation may be quite adequate for describing the depth profiles. The surface value (100% just below the sea surface) is generally derived from the quanta value found above the surface with due regard to the immersion effect and the reflectance at the surface.

The question arises how to express suitably the relationships between the four parameters mentioned $z_{(30)}$, $z_{(10)}$, $z_{(3)}$ and $z_{(1)}$. Since it is in the middle of the photic zone, the 10% level may to advantage be chosen as a reference. Thus in Figures 2 and 3 the levels $z_{(30)}$, $z_{(3)}$ and $z_{(1)}$ are plotted against $z_{(10)}$ for the whole material. The scatter of the points that occurs in these diagrams is in the first place a consequence of accidental errors in the measurements.

Experimental errors

In the first instance the quanta measurements are marred by depth errors even if in many cases depth sensing units have been used. It may happen that disturbances from the ship either by shadowing or by reflection of light against the ship's side influence the results. Waves cause large fluctuations in the upper layers where strong absorption at the ends of the spectrum takes place. It should be observed that properly a mean log value of the fluctuating signal eliminates most of the wave effect. However, the highest level (30%) considered is usually below the most critical zone of wave disturbance and the other levels (10%, 3% and 1%) are little affected by waves.

A major source of error is connected with changes in the angular distribution of radiance from the sky (including the sun) above the sea. With a clear sky the influence of solar elevation is limited to elevations between 90° and 30°; it is of no practical im-

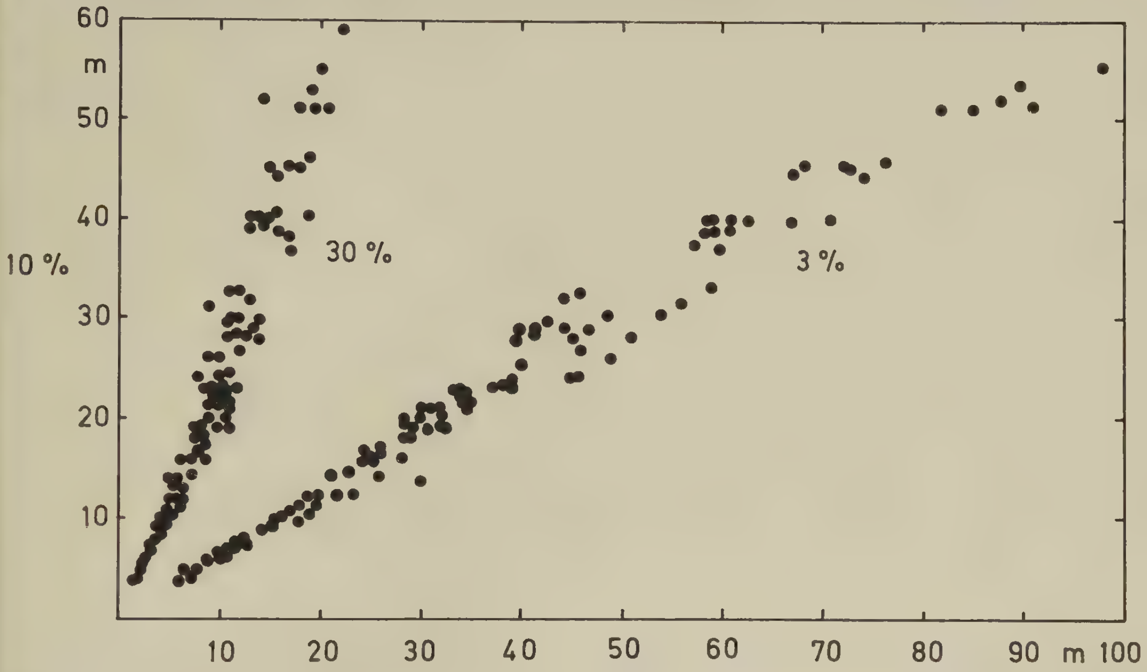

Figure 2. The 30% (of surface quanta) level and the 3% level vs the 10% level.

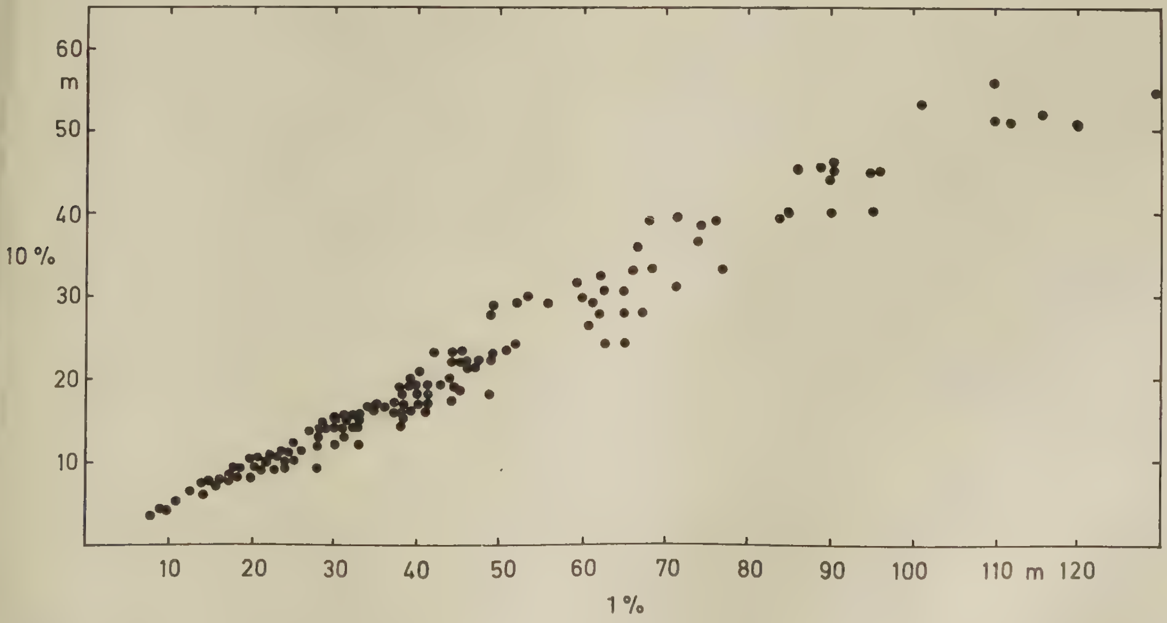

Figure 3. The 1% level vs the 10% level.

portance below 30° (Jerlov and Nygård, 1969a; Højerslev, 1974; Aas, 1976). With an increase in depth the effect is gradually reduced at a rate which is in a complex way dependent on the optical properties of the water as well as on the wavelength. It follows that the relations between the different percent levels must to some degree be influenced by solar elevation. Thus Højerslev (1974) has found by direct measurements in the Mediterranean that, when the sun goes from 73° to 24° elevation, the

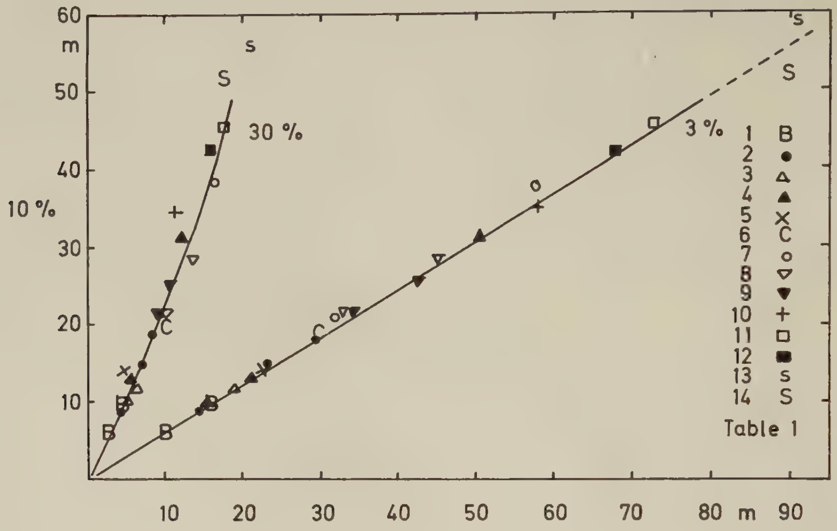

Figure 4. The 30% level and the 3% level vs the 10% level. Mean values for different water masses.

10% level moves upwards from 38 to 30 m but the 1% level from 70 to 64 m only. This is equivalent with a change of the ratio $z_{(1)}/z_{(10)}$ from 1·84 to 2·13 or about 16%.

With changing lighting conditions above the sea a deck photometer is often used for normalization of the observations. It should be observed that the record of such a photometer is not always closely correlated to the variations of the light field at depth: a cloud shadow at some distance from the ship may effect the underwater unit whereas the deck photometer receives full sunlight. Furthermore cloud obscuring the sun can lead to a drastic change in the direction of maximum radiance from the sky.

There is no reason to overdramatize the effect of solar elevation on the relations between percent levels. If a high accuracy is not needed one should not venture an intricate correction of observations with regard to solar elevation.

Classification

A more adequate survey of the experimental data is offered by forming mean values for different areas thus reducing accidental errors (Figs. 4 and 5). On each diagram a line is drawn which is the best fit to the group of points. Deviations from the lines can in most cases be ascribed to measuring errors. It may be noticed that the North Sea points based on a rich material are well on the lines. On the other hand, the deviation for the Drake Passage derived from three measurements only is not evidenced. Attention is drawn, however, to the clear water of Mediterranean at the 1% level which seems to display a real divergence considering that these experiments were conducted under perfect weather conditions and so should be of high accuracy. We shall return to this particular detail.

The result of the data processing is condensed into the three lines in Figures 4 and 5 representing the functions $z_{(30)}/z_{(10)}$, $z_{(3)}/z_{(10)}$ and $z_{(1)}/z_{(10)}$. The two last functions can well be considered as linear even if $z_{(1)}/z_{(10)}$ shows a slight trend ($\pm 3\%$) (see also Table 2); the parameter $z_{(30)}$ is best described by adding a second order term.

Table 2. Levels (m) for different percentages of surface quanta (350–700 nm)

Optical types	30%	10%	3%	1%
I..........	19	49	79	103
IA........	16·5	41	66	87
IB.........	14	33	54	70
II..........	10·5	24	39	52
III..........	6·5	14	23	31
1..........	5·3	12	20	27
3..........	3·7	8·5	14	19
	normalized at 10% level			
I..........	0·39	1	1·65	2·15
IA........	0·40		1·66	2·12
IB.........	0·42		1·63	2·12
II..........	0·44		1·63	2·17
III..........	0·46		1·64	2·21
1..........	0·44		1·67	2·25
3..........	0·44		1·65	2·23
		mean	1·65	2·18

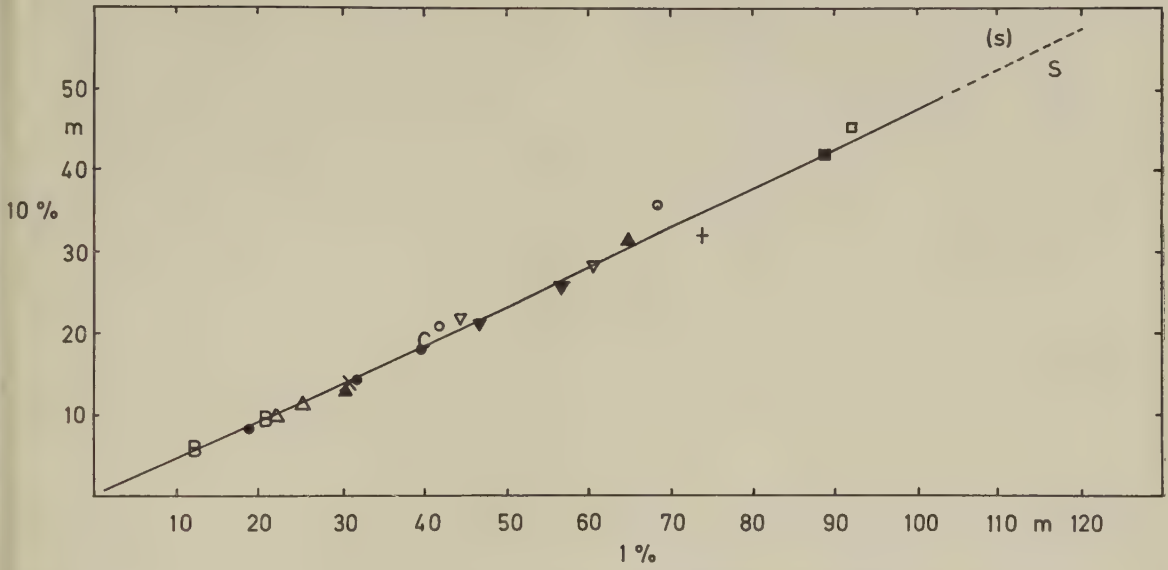

Figure 5. The 1% level vs the 10% level. Mean values for different water masses. Symbols as in Figure 4.

Table 3. Percentage of surface quanta (350–700 nm) at different depths for several optical types of sea water

Depth m	Optical types I	1A	IB	II	III	1	3
0	100	100	100	100	100	100	100
2	79	77	75	70	63	54	44
5	64	59	54	48	38	30	21
10	46	42	38	32	17·5	13·3	7·0
15	35·5	32	28	21	8·5	6·0	2·3
20	29	25·5	21	14·2	4·6	3·0	0·73
30	20	16·4	12·0	6·4	1·22	0·65	
40	13·7	10·3	6·7	2·8			
50	9·5	6·6	3·8	1·23			
60	6·5	4·1	2·0				
70	4·3	2·5	1·01				
80	2·9	1·47					
90	1·85						
100	1·14						

Hence:

$$z_{(30)} = 0{\cdot}50 z_{(10)} - 0{\cdot}0023 z_{(10)}^2$$
$$z_{(3)} = 1{\cdot}65 z_{(10)}$$
$$z_{(1)} = 2{\cdot}18 z_{(10)}$$

This set of equations affords the possibility of determining three percent-levels if one is known. They are also valid for the optical water types defined by the existing classification in terms of spectral transmittance. The characteristic values of the optical types are presented in Table 2; values normalized with respect to $z_{(10)}$ are also given. The debth profiles for quanta irradiance (E_Q) are given in Table 3 and Figure 6 for the oceanic types and for two of the coastal types (1 and 3).

Attenuation coefficients

Some interest is connected with the shape of the curves in Figure 6. A typical feature for clear water is – as mentioned – the double curvature in the profiles

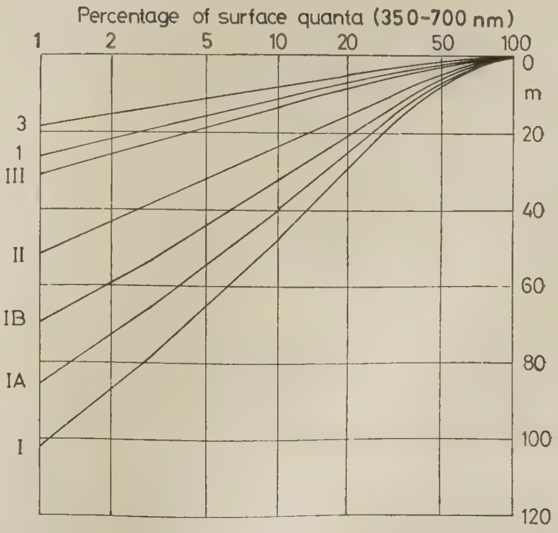

Figure 6. Depth profiles of quanta irradiance (350–700 nm) as percent of surface value for different optical types.

Table 4. Attenuation coefficients (m^{-1}) for different percentage intervals (100% at the surface)

Optical type	100–30%	30–10%	10–3%	3–1%
I	0·063	0·037	0·040	0·046
IA	0·073	0·043	0·048	0·052
IB	0·086	0·053	0·057	0·068
II	0·114	0·082	0·080	0·084
III	0·185	0·146	0·134	0·137
1	0·227	0·164	0·150	0·157
3	0·325	0·229	0·218	0·220

which involves the presence of a minimum in the attenuation coefficient

$$K = -\frac{1}{E_Q} \times \frac{dE_Q}{dz}$$

For types I, IA, IB a marked minimum is found in the interval 30–10% (Table 4); for more turbid water the minimum is weak and seems to occur between 10 and 3%. If instead looking at the coefficient as a function of depth (Table 5) a rather smooth minimum is encountered for Type I; turbid water displays a vague minimum between 15 and 20 m which is not visible on the curves and the reality of which is not clearly established.

Table 5. The attenuation coefficient K_d(m^{-1}) for quanta (350–700 nm)

Depth	Optical types						
m	I	IA	IB	II	III	1	3
0– 2	0·118	0·130	0·144	0·178	0·230	0·310	0·41
2– 5	0·073	0·089	0·107	0·126	0·169	0·196	0·25
5– 10	0·065	0·068	0·071	0·099	0·155	0·163	0·22
10– 15	0·052	0·054	0·061	0·084	0·144	0·154	0·22
15– 20	0·040	0·042	0·056	0·078	0·123	0·140	0·23
20– 30	0·039	0·046	0·057	0·080	0·134	0·153	
30– 40	0·039	0·046	0·058	0·082			
40– 50	0·037	0·045	0·059	0·082			
50– 60	0·038	0·048	0·064				
60– 70	0·040	0·049	0·069				
70– 80	0·040	0·053					
80– 90	0·045						
90–100	0·048						

Discussion

It seems remarkable that quanta irradiance lends itself to a classification through the whole photic zone. For instance, one would not imagine to encounter the same depth profile at a station off West Africa as at a station off Iceland. The objection will immediately be raised that ocean water is not optically homogenous as particle accumulations occur at different levels in the zone. This brings up the problem how the irradiance attenuation is influenced by suspended particles.

The theory of radiative transfer proves that the irradiance attenuation coefficient K is fairly close to the absorption coefficient a for the upper layer (Jerlov, 1976). Therefore, the effect of particles on attenuation is largely due to absorption and in a minor degree to pure scattering. The direct measurements of the ratio a/K carried out by Højerslev (1973) indicate that the ratio for any wavelength generally shows relatively small variations through the photic zone.

In the surface layer of clear water the water itself is dominant in the attenuation coefficient due to the strong water absorption of long wavelengths. With increasing depth the coefficient progressively approaches that for blue light as the water acts as a monochromator. The depth profile for turbid water is nearly a straight line except in the surface layer where the coefficient is high due to absorption at both ends of the spectrum.

Even if the investigation is based on a substantial body of material it cannot be excluded that deviations larger than normal errors may occur. It is for instance indicated that a few points from the Mediterranean show an irregular behaviour. Nevertheless one may venture to assert that the classification in terms of quanta irradiance has met with a reasonable success. The significant aspect is that it allows of describing quanta number as a function of depth in the photic zone with an accuracy sufficient for most practical purposes.

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Fish school acoustic target strength

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Acoustic target strengths of 10 534 fish schools were measured in the California Current system during 6 cruises from November 1974 to October 1975. Measurements were made with a side-looking, 30 kHz sonar with a pulse duration of 10 ms; a separate set of 260 schools were measured with a pulse duration of 170 ms. Peak target strength for the 10 ms data set ranged from −20 to +20 dB with a mean of −7·3 dB (s.d. of 5·9 dB); mean intensity target strength was −2·4 dB. For the 170 ms data set, peak target strength ranged from −10 to +23 with a mean of +1·6 dB (s.d. of 5·6 dB); mean intensity target strength was +4·8 dB. Target strength was found to be dependent on pulse length and range (volume sampled).

Introduction

Many studies have been made of target strength (*TS*) of individual fish (see Love, 1971, for a review), but few measurements of fish school *TS* have been reported. Pickwell et al (1970) measured a *TS* of 0 dB[1] on a school off San Diego, California. They used a 12 kHz source directed vertically down with a pulse duration of 25 ms. McCartney, Stubbs and Tucker (1965) estimated *TS* of 3 pilchard schools off the Cornish coast using a broadband source with peak energy at 1·4 kHz. Their estimated *TS* ranged from −12 to +5 dB. Weston and Revie (1971) estimated *TS* of +5 dB on what they suspected to be pilchard schools in the Bristol channel. Their work was done at 1 kHz.

The data presented here were collected as a cooperative study between the Naval Undersea Center (NUC) and the Southwest Fishery Center (SWFC) of the National Marine Fisheries Service, both located in San Diego. Field work was done during 6 cruises of the Fisheries Service's research vessel, "David Starr Jordan", in the California Current system between November 1974 and October 1975. The area surveyed extended from the coast seaward to 250 miles and was bounded by San Francisco in the north and Cape San Lazaro, Baja California, Mexico in the south.

Schooling, pelagic fish stocks in the California Current system have been described by Mais (1974) in his report on combined acoustic-fishing surveys from northern California to the tip of Baja California, Mexico between 1966 and 1973. He states that results of both acoustic and trawling operations provided overwhelming evidence that the northern anchovy, *Engraulis mordax*, is the most dominant species in terms of biomass in the area. Hence it is reasonable to assume the majority of our targets were schools of *E. mordax*.

Equipment

RV "David Starr Jordan" is equipped with a Simrad Model 580-10 sonar system. The 30 kHz transducer operates from a depth of approximately 4·5 metres and projects a conical beam 10° wide at the 3-dB down points. Full-power, optimum source level is 225 dB// 1 μPa at 1 metre. Received signals are amplified, band-pass filtered, and envelope detected. For this survey, final data processing was done on board, in real time, by a minicomputer system (Digital Equipment Corp. Mod. PDP8I).

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[1] All *TS* values reported herein are in decibels (dB) referenced to a sphere of 2 m radius.

Before each cruise the transducer and receiving system were calibrated in harbour with a test hydrophone. Calibration values measured before the cruise were used to calculate *TS* during that cruise; variations between cruises were less than 2 dB.

Methods

Sonar mapping techniques described by Smith (1970) were used; data were collected only between 0800 h and 1600 h and when the ship was underway at speeds greater than 7 kn (3·6 m/s). The transducer was trained 90° to starboard and tilted to 3° down. A pulse duration of 10 ms and a pulse repetition rate of 1 pulse/s were used. A sampling interval of between 200 and 450 m in range was selected, i.e. no schools between the ship and 200 m in range or with ranges greater than 450 m were sampled. This interval was chosen to maximize the number of targets and minimize acoustic propagation anomalies. Large schools which overlapped the interval at either 200 or 450 m were excluded, resulting in a general undersampling of large schools over the survey.

Ignoring refraction due to changes in sound speed and considering only system geometry, the upper edge of the sound cone intersected the surface at about 130 m in range; at 200 m range the lower edge of the cone was at approximately 37 m in depth and at 450 m range, about 72 m depth. Although downward refraction is predominant in this area, transmission anomalies due to it should be negligible at these short ranges. Thus, most of the schools sampled were most likely in the upper 75 m of depth.

The computer sampled at a rate of 750 samples/s, or one sample/m of range. Criteria used to distinguish schools from spurious targets were as follows. A target threshold (recognition) level was set such that no target with *TS* less than −32 dB would be sampled. For each pulse, signal amplitude of the target had to be greater than this threshold and this amplitude had to continue over 5 consecutive one-m range samples (the latter criterion had the effect of limiting the smallest school we could sample to 5 m in diameter). Also, the target had to meet these criteria over at least 3 consecutive pulses.

Data from 3 consecutive pulses were stored in the computer and as each new data set entered it was examined for targets. When one was present, amplitudes of consecutive pulses were compared and the peak value stored. Peak *TS* and mid-range were then computed and stored in memory; at 1600 h the stored data were printed out on a teletype terminal (see Hewitt, Smith and Brown (1976) for a more detailed description of the data processing system). Peak *TS* was computed from:

$$TS = 20\log(p/p_o) + 40\log R + 2\alpha R \qquad (1)$$

where p is peak backscattered pressure, p_o is transmitted pressure, R is range, and α is the attenuation coefficient (5·5 dB/km). Spherical spreading and a sound speed of 1500 m/s were assumed.

During Cruise 94, a second computer system was used for a preliminary experiment to measure school Doppler. This system controlled pulse transmission to obtain long pulse data needed for frequency spectra analysis without interfering with survey work or overdriving the transmitter. Pulse sequence was changed to 14 short (10 ms) pulses at one second intervals followed by one long (170 ms) pulse, then a 2 second delay and repeat. *TS* sampling by the PDP8I system was not affected except for the slightly diminished sampling time.

Table 1. Dates and results for the six individual cruises and summary results for all cruises. Some long pulse data (170 ms) were collected on cruise 94 and are included for comparison with the 10 ms data from the same cruise. Target strength dependence on pulse duration is indicated. *TS*(dB) is mean target strength; *TS*(*I*) is related to mean intensity measured at the receiver.

"Jordan" cruise No.	Dates Start	End	Year	Number of schools	Sample time (h)	*TS*(dB) (dB)	SD (dB)	*TS*(*I*) (dB)
90	26 Nov	20 Dec	1974	2 407	100	− 7·2	4·9	−4·5
91	20 Jan	8 Feb	1975	2 819	120	− 5·6	5·5	−0·9
92	28 Feb	26 Mar	1975	1 848	102	− 8·4	5·3	−4·4
94	8 May	4 Jun	1975	2 004	90	− 8·3	5·9	−3·9
95	26 Jun	20 Jul	1975	826	82	− 5·6	8·2	+2·0
98	19 Oct	29 Oct	1975	630	30	−10·9	6·0	−6·1
All	–	–	–	10 534	524	− 7·3	5·9	−2·4
94	Long pulse data			260	–	+ 1·6	5·6	+4·8

Results

Table 1 gives results of individual cruises and Figure 1 presents a summary histogram of *TS* in 2 dB cells versus frequency of occurrence for all cruises; statistical determinations are included. There is a difference between mean $TS[\overline{TS}(\text{dB})]$ and mean intensity $TS[\overline{TS}(I)]$ as:

$$\overline{TS}(\text{dB}) = 1/N \sum_{i=1}^{N} TS_i \qquad (2)$$

and we consider $TS = 10 \log I$, where I is the ratio of scattered intensity at one m to incident intensity, then:

$$\overline{TS}(I) = 10 \log 1/N \sum_{i=1}^{N} I_i \qquad (3)$$

This distinction is included, for although $\overline{TS}(\text{dB})$ is the mean of the data presented in Figure 1, $\overline{TS}(I)$ is related to the mean intensity measured at the receiver.

Long pulse data from Cruise 94 are included at the bottom of Table 1. Comparison with short pulse data from the same cruise shows the dependence of peak *TS* on pulse duration. The difference in $\overline{TS}(I)$ for the two data sets is 9 dB, whereas the difference in (10 log) pulse duration is 12 dB. The two data sets are not directly comparable, however, due to sampling differences.

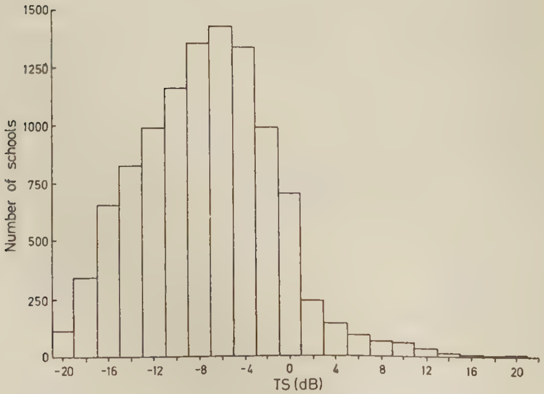

Figure 1. Fish school target strengths (*TS*) in 2 dB cells versus frequency of occurrence; summary data for six cruises in the California Current from November 1974 to October 1975. Pulse duration was 10 ms; frequency was 30 kHz. $N = 10\,534$; $\overline{TS}$ (dB) $= -7{\cdot}3$; SD $= 5{\cdot}9$; $\overline{TS}$ $(I) = -2{\cdot}4$.

Discussion

An attempt to theoretically verify this large set of data seems appropriate, yet many variables are involved in the scattering properties of fish schools of which little is known. Weston (1967) discussed sound scattering by schools of bladdered fishes and showed the scattering cross-section of a school would have a coherent and an incoherent component. Far above the resonance frequency of the individuals in the school, however, the coherent part would become negligible. This is our case, since the resonance frequency of *E. mordax* has been reported by Batzler and Pickwell (1970) to be near 1 kHz.

Considering only the incoherent component, school *TS* becomes:

$$TS = TS_i + 10 \log D + 10 \log V - \text{Attenuation} \qquad (4)$$

where TS_i is the individual school member target strength, D is schooling density in fish/m^3, and V is the volume of the school sampled by the sound cone. Attenuation includes energy lost within the school by scattering and absorption.

Variations in TS_i when fish are rotated through 360° in various planes have been measured in the laboratory (Love, 1971; Haslett, 1969; Shibata, 1971). In each study, variations in TS_i between side aspect and head or tail aspect when the fish were rotated through the yaw plane were 20 dB or greater. Using a 12 cm anchovy (mean standard length of samples from Mais' trawls) and Love's equation for maximum side aspect, TS_i becomes -40 dB. For random aspect encounters with the sonar beam, then, we assume a 12 cm anchovy will have TS_i variations of -40 to -60 dB.

Laboratory studies on schooling density by Van Olst and Hunter (1970) using *E. mordax* indicated that maximum schooling density occurred when there were 0·2 body lengths separating neighbours in the school, and that under normal, monotonous schooling conditions the spacing would be 0·5 body lengths. Assuming that schools are composed of equally-sized individuals arrayed in parallel ranks and files and that the width and depth of a fish equals 0·2 body lengths, schooling density can be approximated from:

$$D = 1/[(d + 1)(d + 0{\cdot}2)^2 L^3] \qquad (5)$$

where d is number of body lengths between neighbours and L is fish length in metres. For 0·2 and 0·5 body lengths, schooling densities for a 12 cm anchovy approximate 3000 and 800 fish/m^3 respectively.

Mais (1974) used school dimensions measured acoustically and purse seine catch data to estimate 50 to 75 fish/m^3 as the most likely range of schooling

Table 2. The sound cone of the sonar divided into one-dB increments of (10 log) volume over the sampling interval (200 to 450 m). Schools were sorted into these range increments and mean target strength [$\overline{TS}$ (dB)] and standard deviation computed for the increment. % N is percent of total schools in the range increment. Dependence of target strength on range (volume sampled) is indicated. Sampling bias of the sampling intervals is evident from decrease in % N at either edge.

Range increment (m)	10 log volume (dB)	$\overline{TS}$ (dB) (dB)	SD (dB)	% N
200–225	39	−16	4·5	4
226–250	40	−14	4·2	12
251–280	41	−11	4·5	15
281–315	42	− 8	4·9	19
316–355	43	− 6	4·8	23
356–400	44	− 4	4·6	19
401–450	45	− 3	7·8	8

density for adult northern anchovy. Graves (SWFC, unpublished MS) used a free fall camera which dropped through anchovy schools taking an exposure each 5 m depth, then returned to the surface. His analysis of photographs from 14 camera drops showed a range of densities from 50 to 366 fish/m^3 with a mean of 115 fish/m^3.

Sample volume is limited by beam geometry and pulse duration for schools larger than the beam, or by school size and shape and pulse duration for those completely inside the beam. The first case can be demonstrated by Table 2 where the sound cone is divided into one-dB increments of (10 log) sample volume from:

$$10 \log V = 10 \log(\pi R^2 \tan^2 \theta C\tau/2) \qquad (6)$$

Where R is the midpoint of the range interval, θ is the half angle of the sound cone at the 3-dB down points (5°), C is 1500 m/s, and τ (pulse duration) is 0·01 s. $\overline{TS}$(dB), standard deviation, and percentage of total schools in the increment are tabulated. This table clearly shows the dependence of peak TS on sample volume. Undersampling of larger schools near 200 and 450 m, as mentioned earlier, is demonstrated by the reduction in total school percentages in the first and last range increment.

Concerning attenuation, Weston (1967, p. 77) suggested that the extinction cross section of a school would likely approach the geometric cross section at higher frequencies and that schools would reflect little or no sound. Davies (1973) measured attenuation through an aggregation of *E. mordax* over the frequency range from 1 to 20 kHz. For his fish density of approximately 650 fish/m^3 the mean one way loss at 20 kHz was 2 dB/m. His results were in general agreement with theory at frequencies above 5 kHz.

The extinction cross section of a single fish (σ_e) will be equal to the scattering cross section (σ_s) at frequencies far above resonance due to the absence of absorption (Weston, 1967), and can be computed from the relationship:

$$TS_i = 10 \log(\sigma_s/4\pi) \qquad (7)$$

For our 12 cm anchovy with maximum side aspect TS_i of −40 dB, σ_e will approximate 10^{-3} m^2; for the minimum TS_i of −60 dB, σ_e will approximate 10^{-5} m^2. The extinction coefficient (K_e) along a path through the school is defined as:

$$K_e = 4{\cdot}34 D\sigma_e \qquad (8)$$

where K_e is in dB/m, D is schooling density in fish/m^3, and σ_e is in m^2.

With consideration for these ranges of uncertainty, we used Equation (4) to estimate limits of school TS. For D we used Graves' mean value of 115 fish/m^3 (21 dB) because it is the only value measured *in situ*. Schools were considered to be spherical and for our smallest school diameter of 5 m, (10 log) volume was 18 dB. For the lowest TS_i of −60 dB, two way attenuation should be small, approximately 0·01 dB/m, and was ignored. At this lower limit, then, school TS becomes −21 dB. At the upper limit, sample volume is beam limited and equals the sample volume at 450 m range (see Table 2) which is 45 dB. With the same schooling density, but with −40 dB anchovies, school TS is +26 dB. Two-way attenuation, however, has increased to 1 dB/m due to increased TS_i, and it can be seen that even slight penetrations into the body of the school will decrease school TS greatly. An increase in schooling density will have the same effect. Thus, we feel our measurements are in reasonable agreement with theoretical considerations of school target strength.

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Salmonid terminology*

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Proposed lists of definitions and terms designating the different life stages of the Atlantic salmon (*Salmo salar*, L.) and the migratory form of the trout (*Salmo trutta*, L.) are presented in English, with equivalents for the basic terms in the languages of the Atlantic salmon and migratory trout-producing countries in Europe and North America. The basic terminology lists include definitions for alevin, fry, parr, smolt, post-smolt, adult fish, previous spawner and kelt for both species.

Part I. A revised terminology list for Atlantic salmon (*Salmo salar*, L.)

Introduction

At the request of the Anadromous and Catadromous Fish Committee of the International Council for the Exploration of the Sea, Allan (1967a) presented a revised terminology list for Atlantic salmon in which the list of common expressions for salmon (*Salmo salar*, L.) originally prepared by Järvi and Menzies (1936) was brought up-to-date.

Contributions to the 1967 revision were received from the following countries: Canada, Denmark, France, Federal Republic of Germany, Netherlands, Iceland, Republic of Ireland, Poland, Spain, Sweden, United Kingdom, United States of America and U.S.S.R. Where no contributions were received it was assumed that no corrections or additions were required by those countries and, therefore, the terms of the original list by Järvi and Menzies were reproduced.

After the 1967 terminology list was produced, further changes occurred in scientific usage and, in 1974, a paper by Ritter and Harger (1974) was presented to the Anadromous and Catadromous Fish Committee, in which refinements to the 1967 list were suggested. As a result, the Committee decided that the present authors should collaborate and prepare a definitive paper for publication. The present paper is the result of this collaboration.

The purpose of the paper is two-fold: first, to enable salmon fishery scientists to interpret correctly the terms used in countries other than their own and, secondly, to propose a terminology for use by scientists and fishery managers.

Review of terminology

The preparation of a terminology list for the life stages of a fish is, to some extent, a subjective exercise if only because different countries use different criteria for their own classifications and because such criteria have different connotations as a result of variations in rates of growth and ages at migration. Therefore, in revising the original list of Järvi and Menzies (1936), we have selected those terms for which the basis is objective rather than subjective while indeterminate descriptive terms such as "under-

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* I. R. H. Allan and J. A. Ritter are responsible for Part I; I. R. H. Allan is responsible for Part II.

Table 1. Revised terminology list for Atlantic salmon (*Salmo salar*, L.)

Stage	Term	Definition
1	ALEVIN	Stage from hatching to end of dependence on yolk sac as primary source of nutrition.
2	FRY	Stage from independence of yolk sac as primary source of nutrition to dispersal from the redd.
3	PARR	Stage from dispersal from redd to migration as a smolt. 0+ parr = parr less than 1 year old (= parr of the year's hatch). 1+ parr = parr 1 year or over but less than 2 years. 2+ parr = parr 2 years or over but less than 3 years. 3+ parr = parr 3 years or over but less than 4 years. Precocious parr = male parr fully ripened or matured in freshwater. Partially silvered parr = parr that are partially silvered and migrating downstream prior to the normal smolt run.
4	SMOLT	Fully-silvered juvenile salmon migrating to the sea.
5	POST-SMOLT	Stage from departure from river until onset of wide annulus formation at the end of the first winter in the sea. ("Pre-grilse" = post-smolt stage returning into freshwater to spawn in year of smolt migration).
6	SALMON	All fish after onset of wide annulus formation at the end of the first winter in the sea.
(a)	1-sea-winter salmon	Salmon which has spent one winter at sea (="grilse" when maturing to spawn).
(b)	2-sea-winter salmon	Salmon which has spent two winters at sea.
(c)	3-sea-winter salmon	Salmon which has spent three winters at sea.
(d)	4-sea-winter salmon	Salmon which has spent four winters at sea.
(e)	Previous spawner	Salmon which has spawned on previous occasion(s).
7	KELT	Spent or spawned-out salmon up until the time it enters saltwater.

yearling" and "fingerling" have been deleted. If terms other than those in this revised terminology list are used in scientific papers, authors are urged to define them carefully.

In the following pages we propose a set of definitions and terms to designate the different life stages of the Atlantic salmon, as summarised in Table 1. The national terminologies for the stages are set out in Table 2.

(1) *Alevin*. The first stage through which the salmon passes after hatching is termed the alevin stage and is usually found within the gravel of the redd. Alevin encompasses the period during which the young fish is dependent upon the yolk sac as the primary source of nutrition.

(2) *Fry*. The term fry has frequently been used to designate the stage lasting from complete absorption of the yolk sac to the end of the first year of post-hatching life. This usage is not appropriate since in those parts of the species range where migration to the sea may take place at the end of the first year of post-hatching life migrants would not have passed through the parr stage between the fry stage and the smolt stage.

We, therefore, suggest that the term fry be used to define that stage beginning with independence from the yolk sac as the primary source of nutrition and terminating with dispersal from the redd. Fry are found over the redd after emergence as alevins from the gravel and are capable of feeding, although vestigial traces of the yolk sac may remain. The duration of this stage is short and normally measured in days.

(3) *Parr*. The parr stage follows next and this starts with dispersal from the redd and continues up to the time the young fish become fully silvered and start their seaward migration as smolts (see below).

The parr stage is often sub-divided according to both age and size. Age-designation is clearly the most precise usage and the terms 0+, 1+, 2+ parr, etc., are commonly used to describe parr of less than 1 year, 1 year or over but less than 2 years, 2 years or over but less than 3 years, etc. respectively.

Size-designation is less precise but may be of more practical value when dealing with large numbers of fish during field surveys for population estimates. Samples collected for such purposes are often divided into 3 categories: 0+ parr, "small" parr and "large" parr. The 0+ parr are fish from the current year's hatch, the "small" parr are those fish which are not likely to become smolts the following spring and are not of the current year's hatch, and the "large" parr are considered to be those fish which are likely to become smolts the following spring. This latter category is usually comprised of fish of different years' hatches but all of which exceed an arbitrary minimum size limit which may vary from river to river.

In some parts of the species range, parr may become partially silvered and migrate downstream earlier than the normal time for the true smolt migration. Such fish should be designed as partially-silvered parr and not smolts.

Also, parr may migrate into and out of various water impoundments at different times; these fish should not be designated as smolts.

Some male parr may ripen or mature during their freshwater residency. These mature parr are known to produce viable sperm and are capable of fertilizing eggs. Such fish are designated as precocious parr.

(4) *Smolt*. The smolt stage is defined as a fully-silvered juvenile salmon during its first seaward migration, normally in the spring, and is capable of surviving transition from fresh water to fully saline water.

(5) *Post-smolt*. The post-smolt stage refers to the juvenile salmon from the time that it departs from the river as a smolt until the onset of wide annulus formation on the scales at the end of the first winter in the sea, when it becomes a 1-sea-winter salmon (see 6, below). However, there are records of return to freshwater in the same year as migration occurred as a smolt. In view of the spawning maturation connotation of the colloquial term "grilse" (see below) the terms "pre-grilse" or pre-1-sea-winter salmon would seem to be appropriate to describe such fish. They are, however, of comparatively rare occurrence in Atlantic salmon.

(6) *Salmon*. The terminologies used for maturing fish returning from the sea to spawn are varied and depend, in some classification systems, on the season of return and in others on the size of the fish, the number of winters spent at sea, or on the age and previous history of the fish as indicated by growth patterns on its scales. Clearly, the latter designation is the most specific, but the more usual designation in common use is that which describes the number of sea-winters. This is more specific than the number of sea-years.

In consideration of the above we suggest that the term salmon should be used to designate all fish after the post-smolt stage. Age should be defined by the number of winters elapsing since the fish entered the sea as a smolt.

The colloquial term "grilse", representing a salmon which has first matured, or is about to mature, after one sea-winter is strongly entrenched in common use and in the literature. However, this term is a source of inaccuracy as it is frequently applied to salmon within an arbitrary length or weight range which may include fish of different sea-ages. Therefore, we recommend that if the term "grilse" is used instead of the more precise sea-winter terminology, it be initially defined.

The term "grilse" has a maturation connotation and it should not be used for 1-sea-winter salmon caught during the marine feeding phase. Such fish may not be maturing to spawn but be destined to spend a second winter (or more) at sea before doing so. Salmon of 2 or more sea-winters, as a group, should be referred to as multi-sea-winter salmon.

The extent to which the salmon sea-winter age-classes are segregated on entering the rivers as distinct seasonal "runs" in spring, summer and autumn or fall varies widely. All, or only some, of the seasonal runs may be present and one or more runs may predominate. In those United Kingdom rivers classed as "grilse rivers", for instance, the 1-sea-winter fish predominate and enter the river mainly as a summer run but may continue to arrive as late as the spawning months.

When the year-class composition of a seasonal run is sufficiently well established such seasonal terminology may have some value, in view of the genetic and feeding migration implications for stock management. Where such seasonal terms are used, however, they should always be carefully defined initially because salmon of different sea-winter age-classes can overlap considerably in their run timing.

The descriptions "small" or "large" for salmon are subjective and thus imprecise and should be avoided. If such terms have to be used to indicate loose groupings of individuals – for instance in reporting a sport or commercial catch for which identification of age-classes may not be possible – the ranges of lengths or weights used within the groupings should be specified. Classification of salmon by weight or length is also imprecise in that a considerable overlap for the various sea-winter age-classes can occur.

Salmon of any age-class which are maturing to spawn for the first time are described as "maiden" or "virgin" salmon.

Salmon of any age-class which are maturing to spawn for a second (or subsequent) time are referred to as "previous spawners". We have chosen the word "previous" rather than "repeat", even though the latter is widespread in current usage. The term "previous spawner" applies to fish at any time after initial spawning whereas the term "repeat spawner" is only appropriate when describing fish that have actually spawned the second time (or more).

The terminology of fish with a spawning history should take into consideration: (i) the sea age of the fish at initial spawning, (ii) the temporal pattern of the subsequent spawning migrations, and (iii) the number of previous spawnings.

It is suggested, therefore, that previous spawning fish be categorized according to their designation of first spawning. Thus, a fish which spawned initially as a 1-sea-winter salmon (grilse) remains a 1-sea-winter salmon (grilse) throughout its subsequent history and is, accordingly, designated as a previous spawning 1-sea-winter salmon (previous spawning grilse). Older previous spawning salmon can be designated similarly.

The proportion of Atlantic salmon which spawn a second time is variable; in some stocks they make a significant contribution, in others they are rarities. The proportion which spawn a third or fourth time, however, is very small. It is considered, however, that as considerable interest attaches to these multiple spawners some system of terminology should be applied to them.

The temporal pattern of successive spawnings is frequently consistent for an individual fish in that it spawns every year or every other year. Fish attaining sexual maturity in these two patterns are designated as consecutive or alternate spawners, respectively. Other descriptions in common use are short-absence and long-absence for fish which return to spawn in consecutive or alternate years, respectively.

Until first spawning, the use of sea-winters to designate the age of the fish is unequivocal but because the winter during which spawning takes place may be spent wholly in the river and not in the sea the designation of the fish's age thereafter in terms of sea-winters could be a technical misuse of the term.

In the case of a multiple spawner, for instance, there will have been 1 or more pre-spawning sea-winters followed by either a succession of river winters (successive spawner) or an alternation of river and sea-winters (alternate spawner).

To devise a special nomenclature to take account of these behaviour patterns in expressing the total age of the fish would be cumbersome and, indeed, some salmon which spawn early in the season (e.g. November) return quickly to the sea as kelts and therefore spend most of their spawning winter back in the sea.

It is proposed, therefore, that the designation of total age in the terms already suggested indicates adequately the history of the fish. For example, a "2-sea-winter previous spawner, 2 consecutive spawnings" would indicate a fish which returned to spawn initially after 2 winters in the sea, and spawned twice more, in each of the years following the initial spawning year, i.e. a five-year old salmon (ignoring the pre-smolt river years); whereas a "2-sea-winter previous spawner, 2 alternate spawnings" would indicate a fish which returned to spawn initially after 2 winters in the sea and spawned twice more in alternate years following the initial spawning year, i.e. a seven-year old salmon.

A fish which changed its return habit would be described as a "2-sea-winter previous spawner, 1 consecutive 1 alternate spawning" or a "2-sea-winter previous spawner, 1 alternate 1 consecutive spawning", both indicating a six-year old salmon and the order in which the spawning habit had altered.

This terminology would thus tacitly accept that the spawning winter, or a part of it, had been spent in freshwater.

(7) *Kelt.* Among fishery workers disagreement exists over the definition of the term kelt. All agree that this term refers to a spent or spawned-out salmon but disagree about the termination of the stage. According to some individuals, viewing the salmon as a marketable food item, a spawned-out salmon ceases to be a kelt when it has recovered the condition and weight lost during and following its spawning migration. Other individuals state that a spent salmon ceases to be a kelt when it re-enters salt water. We tend to agree with the latter definition as it is more specific than the former and is more meaningful in light of the physiological changes that take place with re-entry into salt water (i.e. re-acclimation, beginning of feeding and replacement of weight lost and silvering).

Because the two definitions for the term kelt are likely to cause misinterpretation, we urge authors to define the term carefully when it is used initially.

(8) *Fish culture terminology.* The terminology used in fish culture may be different from the above and is likely to be more detailed and chronological in relation to the early developmental stages. However, for the sake of uniformity it is recommended that, so far as is possible, the terminology used by fish-culturists follow that set out in this paper.

other experiments. More elaborate subdivision of the early life stages may, however, be necessary for hatchery purposes.

Acknowledgments

The authors wish to acknowledge the assistance of members of the Anadromous and Catadromous Fish Committee in making their lists of national terminologies available. They also wish to acknowledge the assistance derived from discussions with their colleagues and particularly Mr A Swain, in London, and Mr J. R. E. Harger, in Halifax.

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The relationship between infestation by *Mytilicola intestinalis*, Steuer (Copepoda, Cyclopoidea) and the condition index of *Mytilus edulis* in southwest England

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Seasonal cycles in the condition index of *Mytilus edulis* from three sites in southwest England are described. These are analysed in relation to host length, stage of gonad development and parasite burden by linear regression analysis. An effect on the condition index due to the presence of *Mytilicola intestinalis* can be detected only in the sublittoral mussels in those few winter months when the mean intensity of infestation is over about 25 parasites per host. In all cases studied, the magnitude of the effect due to variation in host length, stage of gonad development, seasonal cycles and environmental factors is greater than that due to parasitism.

Introduction

The collapse of the Dutch mussel fishery in 1949 (Korringa, 1950) stimulated research into the possible effects of *Mytilicola intestinalis* on its host *Mytilus edulis*. Meyer and Mann (1950) came to the conclusion that an infestation of more than three parasites per host increased protein digestion and respiration rates while at the same time depressing filtration rate and therefore food intake, so creating a negative energy balance which caused loss of condition and, with severe infestations (more than eight parasites) probably death. At the same time, Cole and Savage (1951) concluded from studying a sample of mussels from Blyth and Conwy that the presence of *Mytilicola* was associated with a serious reduction in condition in infested mussels, and Odlaug (1946) came to the same conclusion for oysters from Puget Sound infected with *M. orientalis*.

On the other hand, Hepper (1955) found that the presence of quite high infestations of *Mytilicola* did not necessarily reduce the condition of mussels and concluded that if environmental conditions were good, mussels could easily withstand quite heavy infestations. Williams (1969), in an analysis of the annual fluctuations of the biochemical constituents of infested and uninfested *Mytilus* from Lee-on-Solent, could not detect a general difference between the two types of mussels except perhaps for a slightly slower recovery rate of infested mussels after spawning. More recently, Dethlefsen (1975) analysed the relationship between meat content and degree of infestation by *Mytilicola* for intertidal and sublittoral mussels in the Waddensee. Using linear regression analysis he could find no statistically significant correlation between these two factors.

Thus there appears to be a conflict of opinion on the question of whether the presence of *Mytilicola* affects the general condition of mussels. Most of the early workers confined their study to one or two samples, often from different sites, at one particular time of year and did not look at the relationships between conditions and other host variates such as length, sexual development and the size of the parasite population over an extended period. During a two-year study of the host-parasite relationships in mussels from three sites around Plymouth, the examination of monthly samples of both host and parasite populations produced data from which it was hoped that the relationships between condition index and parasite numbers could be elucidated.

Methods

Sampling

Between January 1974 and December 1975, monthly (or occasionally bi-weekly) 0·1 m^2 samples of mussels were taken at MLWS tide level on Beggars Island

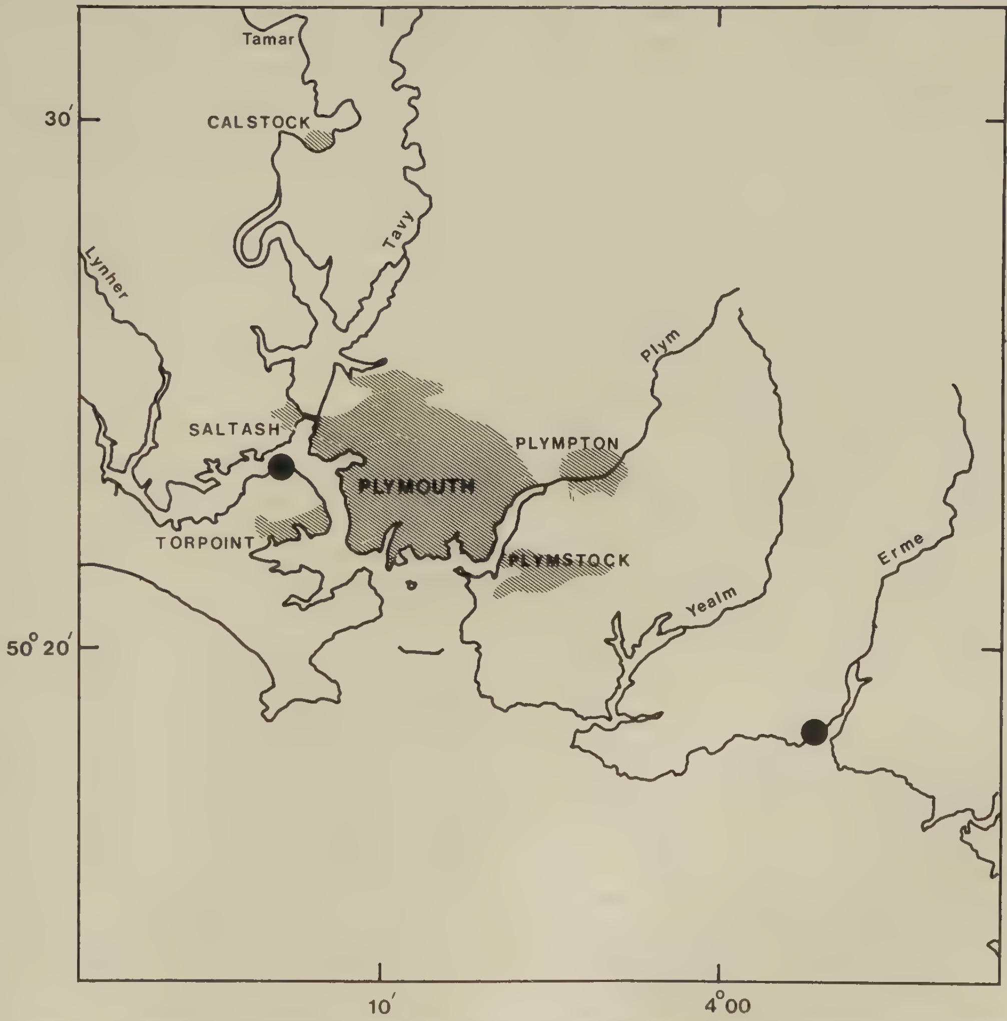

Figure 1. A map of the Plymouth area showing the general location of the sampling sites (black circles).

(see Fig. 1) at the mouth of the Lynher River (O.S. Grid Ref. SX 423575). These were washed and sorted into 2·5 mm length groups and a subsample of 50 was then taken, such that the length groups of mussels larger than 20 mm were represented in proportion to their abundance in the total sample. The subsample was kept in a re-circulating aquarium system until it could be examined, usually within one or two, and never more than four, days after collection. The same mussel bed extends below ELWS tide level and each month between October 1974 and September 1975 a sample of 50 mussels was taken with a 45 cm naturalist's dredge from the sublittoral part of the bed and treated in the same way as the littoral subsample. A small bed of mussels in the River Erme estuary (O.S. Grid Ref. SX 613473) which was used as a source of uninfested mussels for experimental work, was also sampled at bi-monthly (and occasionally monthly) intervals in the same manner as the Beggars Island littoral mussels.

Host data

Epibionts were removed from each mussel by scraping the shell with a scalpel and then rinsing the mussel in fresh water. The following data were then obtained:

Length. Each mussel was measured to the nearest 0·1 mm.

Sexual state. After removal of the left-hand shell, the gonad was examined under a binocular microscope and the stage of development assessed according to the following criteria:

I. *Immature*, in which there was no sign of developing gonadal tissue in mussels less than about 30–35 mm,

II. *Resting*, in which the gonadal tissue was transparent or semi-opaque but in which no developing gametes were obvious,

III. *Developing*, in which gametes were present in the gonads but upon cutting the tissue with a scalpel were not released,

IV. *Ripe*, (sexed into male and female) in which on cutting the tissue with a scalpel, ripe gametes were released,

V. *Spent*, in which the gonads were watery and transparent but usually with a few unreleased gametes remaining.

For the analyses in this paper, stages II and V have been combined as it was often difficult to tell the difference between them, and because V appears to pass fairly rapidly into II.

Condition index. An adaptation of the method described by Baird (1958) was used. Before a mussel was opened, its total volume was measured by displacement of fresh water in the smallest measuring cylinder (to BS 604) which would receive it. After all the contents had been removed, the volume of the shell alone was estimated by the same displacement method. The contents of the shell, minus parasites and byssus threads, were placed in small, numbered, weighed glass dishes and dried for 24 h at 105° before being reweighed. The condition index is calculated as $\mathrm{CI} = 10^3 \times$ dry weight of flesh (g)/volume of shell cavity (ml).

Parasite data

The alimentary tract was opened *in situ*, starting at the rectum. All parasites were removed, counted and preserved in 5% formolsaline before being sexed and measured.

Statistical analysis

The sampling procedure was not designed specifically for this study. As a result there were often no specimens, or insufficient numbers, in some of the groups and it was therefore necessary to use multiple regression analysis rather than the analysis of variance. The analyses were performed using the method of Snedecor and Cochran (1967) for multiple regressions. For the regressions which were performed on the total grouped data for each site (Table 1) the data for sexual stage and condition index were corrected for seasonal cycles by reducing the data to their deviation from the mean of each sample. The results of regression analyses for data transformed to $\log_{10}(x + 1)$ were not significantly different from those carried out on the basic data. For clarity of presentation only the untransformed figures are given in this paper.

Results

The annual cycles of parasite burden and condition index for the mussels from the three sampling sites are shown in Figure 2. Infestation levels were extremely low in the River Erme mussels; the few parasites that were found there occurred during the autumn and winter months. At the two sites in the River Lynher the sublittoral mussels were much more heavily infested than the littoral mussels but the general pattern of changes in parasite burden was the same, being highest in the early winter and lowest in the early summer with an approximately five-fold difference between summer and winter.

The cycles of condition index were similar at all three sites, the peak condition being reached in the late summer and autumn, followed by a decline through the winter to early spring, after which there was a rapid recovery. Slight differences between the cycles in the Erme and Lynher are probably related to differences in the timing of spawning. In 1974 the littoral mussels in the Lynher River spawned early in the year and, as is sometimes the case when this happens, there was a second, smaller spawning in the autumn. The River Erme mussels on the other hand spawned in the spring and did not have an autumn spawning. At all sites, there was approximately 40% loss in condition, from the peak condition in the late summer of 1974 to the time of spawning in the spring of 1975 but following this, much higher condition indices were reached than in 1974, probably as a result of the higher summer temperatures which prevailed during 1975.

Table 1 gives the correlation coefficients of a linear regression analysis of each pair of the four variates (length, sexual state, number of parasites and condition index) in all samples combined from each of the three sampling sites. In view of the large size of the samples ($n = 1486$ for Lynher littoral, $n = 543$ for Lynher sublittoral and $n = 738$ for River Erme) only those values of r for $P < 0{\cdot}01$ are regarded as

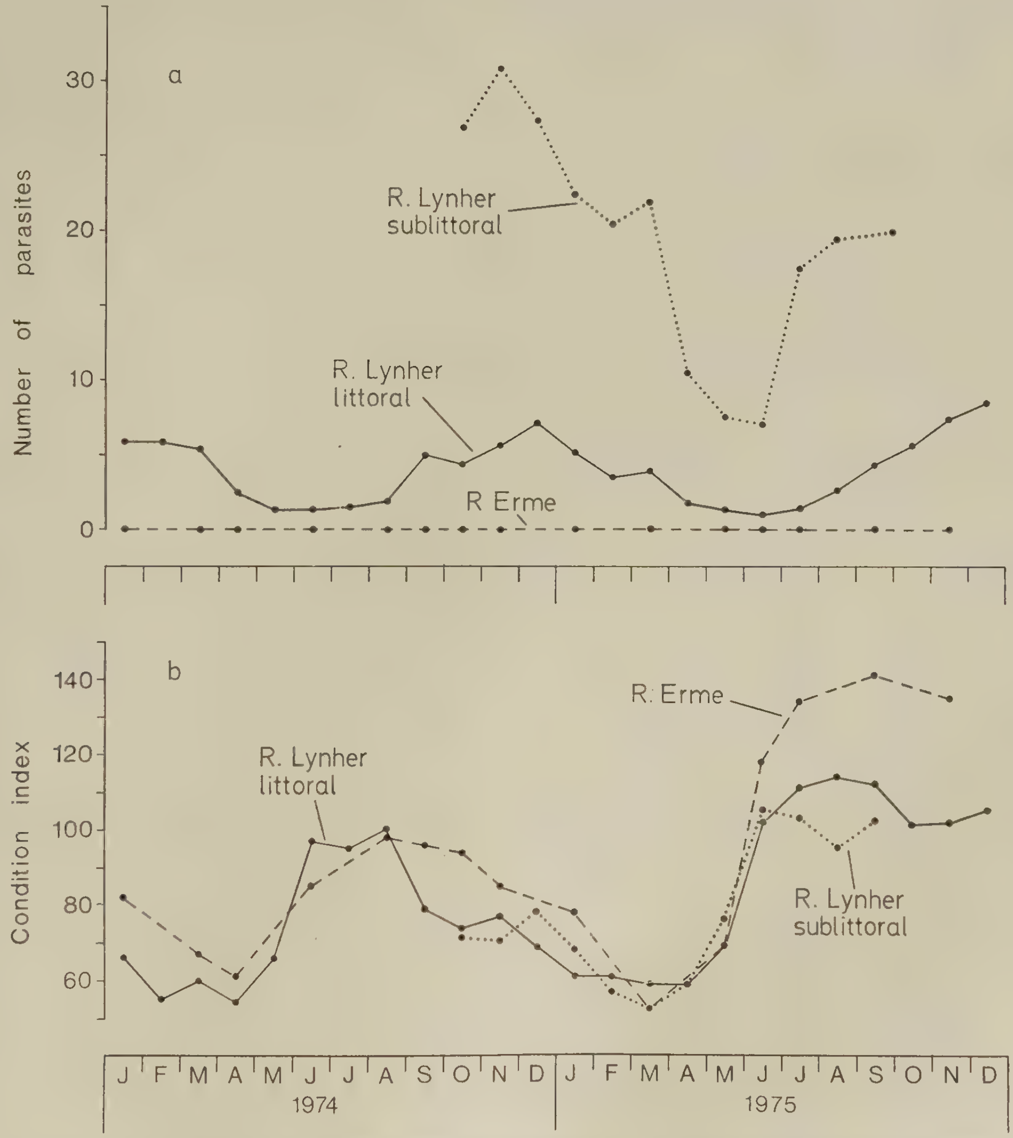

Figure 2. Monthly values for (a) mean number of parasites and (b) mean condition index of mussels from the River Lynher littoral site (solid lines); the River Lynher sublittoral site (dotted lines) and the River Erme site (dashed lines).

significant. The results show that at all three sites sexual state was correlated with length and condition index with sexual state. In the littoral and sublittoral samples from the Lynher River, condition index and parasite numbers were both correlated with length. As expected no evidence of a correlation was found between number of parasites and sexual state but there was evidence of a correlation between condition index and number of parasites in the heavily infested Lynher sublittoral mussels.

In a further analysis, multiple linear regression equations for condition index in terms of the other three variates were fitted to each of the monthly samples for each of the sampling sites. The results are given in Table 2, which shows the percentage of the variance accounted for by each of the variables. It must be pointed out here, however, that two of the prerequisites of this method were not strictly met by the present data. Firstly all the variables were not independent of each other in that almost all mussels

Table 1. Infestation of mussels with *Mytilicola*: correlation coefficients of regression analysis of each pair of variates, all samples combined for each locality.
* 0·05 > *P* > 0·01 ** 0·01 > *P* > 0·001 *** *P* < 0·001.

	Sample site	Length	Sexual state	Condition index
Sexual state	R. Lynher littoral...........	0·213***		
	R. Lynher sublittoral........	0·188**		
	R. Erme..................	0·554***		
Condition index	R. Lynher littoral...........	−0·308***	0·186***	
	R. Lynher sublittoral........	−0·225***	0·253***	
	R. Erme..................	0·069	0·191***	
No. of parasites	R. Lynher littoral...........	0·237***	0·072	−0·074
	R. Lynher sublittoral........	0·233***	0·035	−0·168**
	R. Erme..................	0·043	0·008	0·031

Table 2. Infestation of mussels with *Mytilicola*: percentage of variance in condition index accounted for by addition of each variate in the multiple regression. Signs given are those of the multiple regression coefficients.

Sample Date 1974–5	R. Lynher littoral			R. Lynher sublittoral			River Erme		
	Length	Sexual state	No. of parasites	Length	Sexual state	No. of parasites	Length	Sexual state	No. of parasites
Jan......	− 7·51**	+11·29***	−0·39	–	–	–	+ 4·00	+24·09***	−0·002
Feb......	+ 3·19	+43·88***	+0·70	–	–	–	–	–	–
Mar.....	− 5·23	+31·94***	−0·99	–	–	–	+48·71***	+ 1·11	−0·86
Apr......	− 4·80*	+21·57***	+1·39	–	–	–	+35·79***	+ 7·96	+2·01
May.....	− 9·40**	+16·67***	−0·15	–	–	–	–	–	–
Jun......	−15·66***	+ 5·87*	+0·57	–	–	–	−23·61***	− 2·35	–
Jul......	−16·91***	+ 0·91	+0·05	–	–	–	–	–	–
Aug.....	−18·49***	+ 1·14	−0·91	–	–	–	+ 4·73	− 6·07	–
Sep......	− 4·38	+14·94**	+3·06	–	–	–	−20·05**	+ 1·19	+1·85
Oct......	−33·66***	− 6·81	−0·05	− 5·59	+17·68**	−18·30**	–	–	–
Nov.....	−12·01*	+20·42**	−0·19	−17·29**	+ 0·32	−11·00*	−10·12*	+15·16**	–
Dec......	−14·85**	+31·56***	−1·07	− 0·93	+28·91***	− 0·003	–	–	–
Jan......	− 0·004	+38·73***	−2·82	− 0·42	+48·85***	− 0·04	+34·62***	+18·68**	–
Feb......	−35·17***	+39·06***	+0·58	− 2·91	+48·72***	− 0·34	–	–	–
Mar.....	−20·49**	+13·98**	+1·00	− 1·74	+50·12***	− 0·04	+20·95**	+11·79*	–
Apr......	−24·81***	+26·93***	−0·02	−20·15**	+14·81**	− 0·001	–	–	–
May.....	−41·13***	+ 6·86	−0·07	−13·61**	+19·56**	− 1·89	−32·47***	+ 9·30*	–
Jun......	−31·81***	+20·29**	−3·52	−24·52***	+ 0·06	− 2·71	−22·67***	+ 5·40	+0·07
Jul......	− 4·95	+ 6·13	+0·15	−16·88**	+ 0·60	− 4·75	−31·54***	+ 3·02	–
Aug.....	−28·33***	+ 6·60	−0·32	− 1·22	+ 2·45	− 5·49	–	–	–
Sep......	− 5·89	+ 0·03	−1·93	−20·58**	+ 5·16	− 0·001	− 0·29	+ 5·16	–
Oct......	−17·75**	− 1·65	−0·64	–	–	–	–	–	–
Nov.....	− 5·62	+15·76**	−0·002	–	–	–	–	–	–
Dec......	− 0·06	+48·17***	−1·44	–	–	–	–	–	–

below 30–35 mm were immature and, in theory, larger mussels are capable of carrying more parasites than smaller ones. Thus the order in which the variables were entered in the analysis may affect the value obtained. However, in trials on the Lynher sublittoral samples (i.e. the most heavily infested ones) in which different combinations of order of entry into the regression equation were tested, the values obtained showed close agreements, thus indicating a high degree of independence of the variates over the ranges encountered in the present study. The second difficulty, which also applies to the simple linear regression analysis, was that the value for sexual state is, strictly speaking, a non-parametric statistic, unless the time span of each stage is approximately the same; stage IV tended to be shorter than any of the other stages.

Bearing these drawbacks in mind, Table 2 indicates that in the Lynher littoral mussels, variations in host length explained a significant part of the variance of the condition index in 16 of the 24 months, the months of no significance generally being in winter when the size range of hosts was smallest (although mean host size varied very little throughout the year).

The effect of sexual state on condition index was significant from November to June each year, that is, during the months up to, and including, the spring spawning when the sample range of development of the gonads was at its greatest. The range of parasite burdens found in any month of the year had no effect on the condition index of the host.

In the Lynher sublittoral mussels, the effect of host length and sexual state on the condition index was very similar to the littoral samples, but the non-significance of length in relation to condition index in the winter months was even more marked. It must be remembered, however (see page 301) that, as a result of the sampling technique employed, the size range of hosts in the population was not necessarily adequately represented in the sublittoral samples. The number of parasites per mussel in the Lynher sublittoral population was much higher throughout the year than in the littoral population but Table 2 suggests that the significant relationship between number of parasites and condition index (indicated in Table 1) existed only during the late autumn and early winter months when the parasite population was at its maximum (in November 1974 the mean number of parasites per host was 31 and the range from 3 to 92). This relationship does not appear to be consistent, however, as infection levels in December were as high as in the two previous months but no evidence of an effect of parasite burden on condition index was indicated for that month.

In order, therefore, to confirm that the multiple regression analysis was giving the correct results for the relationship between parasite numbers and condition index (in view of the drawbacks mentioned above), simple linear regressions between these two variates were performed for the three months of highest and lowest infestation levels in the Lynher sublittoral samples and the Lynher littoral samples. The results are shown in Table 3. The correlation coefficient of the regression was significant ($P < 0{\cdot}01$) in the Lynher sublittoral sample for October when host size and sexual stages were ignored. In this month sexual state had a significant effect on condition index (as shown in Table 2) and when this effect was eliminated by treating mussels of different stages of gonad development separately, it was found there was still a significant correlation between number of parasites and condition index in mussels in stage III of gonad development. A similar result was also obtained with the November sample, but here the effect of length was eliminated (shown to be significant in Table 2). In this month there was a significant correlation ($P < 0{\cdot}05$) between parasite numbers and condition index in the 60–69 mm size group of mussels. No correlation was found in December, even when host size and sexual state were ignored. A correlation was indicated in May when host size and sexual state were ignored. However, Table 3 shows that there was a large difference in mean parasite burden for two of the size groups of hosts in the

Table 3. Regression analysis of number of parasites and condition index for specified groups of mussels from the Lynher River

Monthly sample	Host size	Sexual stage	Parasites		Condition index		Correlation coefficient	DF ($N-1$)
			Mean *n*	SD	Mean *n*	SD		
R. Lynher sublittoral								
Oct 1974...........	All	All	27·1	12·7	71·4	28·2	0·36**	48
	All	III	25·7	12·4	87·6	30·4	0·56**	22
	All	II	27·2	12·0	54·3	15·6	0·28	19
Nov 1974...........	All	All	31·0	17·2	70·7	32·5	0·43**	47
	60–69 mm	All	29·8	19·9	70·3	33·7	0·43*	17
	50–59 mm	All	32·6	15·7	76·3	34·1	0·36	18
Dec 1974...........	All	All	27·4	13·6	77·9	29·7	0·13	47
Apr 1975...........	All	All	10·5	8·8	59·2	30·4	0·12	49
May 1975...........	All	All	7·6	7·1	75·5	24·5	0·34*	49
	60–69 mm	All	12·0	8·5	69·4	12·0	0·35	15
	50–59 mm	All	5·3	4·2	83·6	30·5	0·19	16
Jun 1975...........	All	All	7·0	4·5	105·2	28·9	0·26	48
R. Lynher littoral								
Nov 1974...........	All	All	5·6	2·7	69·9	23·3	0·15	46
Dec 1974...........	All	All	7·1	3·1	69·0	23·0	0·14	48
Jan 1975...........	All	All	5·3	3·2	62·1	20·7	0·08	49
May 1975...........	All	All	1·4	1·5	69·4	14·7	0·01	49
Jun 1975...........	All	All	1·1	1·0	108·3	31·7	0·18	49
Jul 1975...........	All	All	1·4	1·4	110·1	33·3	0·01	48

sample, and when the effect of host size was eliminated there was no significant correlation between parasite burden and condition index.

In the River Erme, the mussel population was virtually uninfested and was found in an entirely different habitat from the Lynher mussel population. The relationship (Table 2) of sexual state to condition index, however, followed a similar pattern to that described for the Lynher but this was not the case with the relationship between length and condition index. Table 1 indicates that these two variates were not significantly correlated in the Erme samples. Table 2 however, shows that on a monthly basis there was almost always a significant correlation but that during the winter the correlation was positive and during the summer it was negative (in the Lynher the correlation was almost always negative).

Discussion

The form of the seasonal cycle in condition index shown in Figure 2 was similar to the cycle of organic dry weight of mussels from the Conwy area given by Dare (1973) who found that maximum meat content for a given size was attained during the summer and autumn and that there was a decline of approximately 40% up to the time of spawning in the late spring and early summer. Similar results were also obtained by Williams (1969) for various biochemical components, particularly carbohydrates, in mussels from Lee-on-Solent and by Hancock and Franklin (1972) for cockles in the Burry Inlet. These studies suggest, along with the present one, that the cycle of gametogenesis is the main cause of seasonal variation in condition index of *Mytilus*. The unexpectedly sharp decline in condition index in the Lynher littoral mussels in the autumn of 1974 was probably due to a second, smaller spawning which took place at that time.

It is well-known that condition index is correlated with length of mussel but the results from the River Erme indicate that this is not always a constant relationship. It is postulated that variations in the length-frequency composition of the population, coupled with relative spawning potential of the various size groups of hosts, are responsible for this. The length frequencies of a winter sample and a summer sample of mussels from the River Erme are given in Figure 3. In summer a large proportion of the mussels were less than 40 mm in length and, from the state of development of the gonads, it seemed likely that relatively few of these small mussels spawned. In the immediate post-spawning period, therefore, these mussels were likely to have a higher condition index than the spawned mussels and a negative relationship between length and condition index for the population as a whole would result. In the winter samples, the 50 mm size group had presumably recovered from spawning and built up reserves for the production of gametes. This, coupled with the low numbers in the smaller size groups in the population produced a positive relationship between condition index and length. The length frequencies in Figure 3 suggest that mussels survive only for approximately three years in the River Erme. In the Lynher, however, during the course of the present study, the majority of the population throughout the year were over 60 mm in length and almost certainly older than the Erme mussels (although Seed, 1968, has shown that the age-length relationship is not the same for all populations). Senescence may therefore have been a factor which reduced the condition index of the largest mussels in the Lynher and so produced a generally negative relationship between length and condition index in this population.

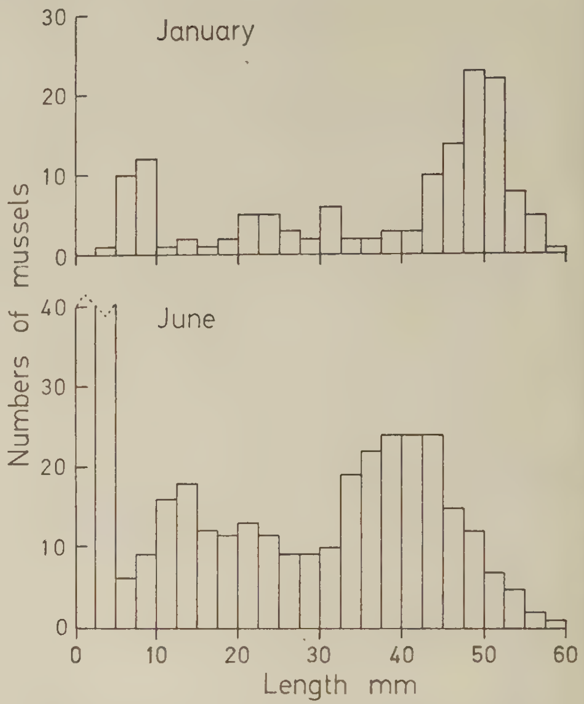

Figure 3. Numbers of mussels by 2·5 mm size groups in January and June samples from the River Erme site.

An effect on the condition index of mussels due to the presence of parasites has been detected in the Lynher sublittoral mussel population only in the first two of the three months (October–December) of the year when the average number of parasites per host was over 25. However, the fact that no significant effect was detected in December suggests that the response may not be due simply to the presence of high numbers of parasites. Campbell (1970) has suggested that the early larval stages, which inhabit the stomach and digestive tubules cause the most damage. The results of a number of transplant experiments, and of an analysis of the developmental stages of the *Mytilicola* in the samples used in this study (which illustrate the pattern of monthly recruitment to the parasite population in the Lynher) showed that August–November was the period of greatest larval influx and that recruitment usually fell sharply in December. Thus it would appear that a combination of the presence of a large number of parasites, and a high proportion in the early stages of development, may have been responsible for the significant effect of parasites on condition index in October and November 1974, as demonstrated in Table 3.

These levels of infestation (a mean of over 25 parasites per host) are much higher than those normally encountered in mussel populations in heavily infested areas such as the southwest of England (Davey and Gee, 1976). They are certainly much higher counts than were found in Dutch mussels (Korringa, 1950) or at Whitstable (Williams, 1969) at the time of the decrease in these fisheries. It seems unlikely therefore that the presence of *Mytilicola* was the direct cause of the mortalities encountered in these areas. Dethlefsen (1975), in his study of littoral and sublittoral mussels in the Waddensee, found that in general the meat content of littoral mussels was lower than that of sublittoral mussels but in neither group could he detect any effect due to the presence of parasites in any month of the year. The infestation levels in both his populations were also higher than in Dutch mussels in 1950 and were slightly higher than those for the Lynher littoral samples. Cole and Savage (1951) examined a single sample of 50 mussels of lengths 55–59 mm, collected from Blyth, Northumberland, in January. They found a decrease in mean parasite numbers with an increase in 0·5 g weight groups. We have subjected the data in Tables 1–6 of Cole and Savage's paper to one-way analysis of variance [after a $\log_{10}(x + 1)$ transformation of the parasite counts] and the results are shown in Table 4. Bartlett's test for homogeneity of variance was not significant. The analysis was therefore valid but $F = 2{\cdot}33$ was not significant. Thus the conclusion of Cole and Savage that the parasites were having a profound effect on the condition of mussels is questionable, especially when it is remembered that no account is taken of the stage of gonad development and that the Blyth sample was collected during the winter when the present data show that sexual state is correlated with condition index (or meat content). The mean parasite burden for the sample is 18 per host, higher than Dethlefsen's highest figure but much lower than the level at which parasites might begin to affect condition in the Lynher sublittoral samples.

Table 4. Analysis of variance of transformed data [$\log_{10}(x + 1)$] of Cole and Savage (1951) on the number of *Mytilicola* in various flesh weight groups of 55–59 mm *Mytilus edulis* from Blyth, Northumberland

Wt. group (g)	n	Transformed mean No. of parasites	Standard error
2·0–2·45	8	2·97	0·232
2·5–2·95	12	3·02	0·190
3·0–3·45	10	2·80	0·208
3·5–3·95	13	2·45	0·182
4·0–4·45	4	2·43	0·329
4·5–4·95	3	1·89	0·379

$F = 2{\cdot}334$ df : (5, 44)

In conjunction with the present study, Moore et al (in press) and Bayne et al (in press) have studied the effects of *Mytilicola* on the histology, histochemistry and physiology of *Mytilus*, in relation to other environmental stress factors, particularly temperature and food supply. These authors' findings do not support those of previous workers (e.g. Meyer and Mann, 1950) and they have concluded that *Mytilicola* has little or no effect on the general performance of *Mytilus*. A decrease in filtration rate is the only detectable effect at infestation levels comparable to those of the winter Lynher sublittoral samples but even then the effect is small compared to that which is produced by subjecting infested and uninfested *Mytilus* to thermal and/or starvation stresses.

It may be concluded that over the range of parasite burdens normally found in Britain, the presence of *Mytilicola* has little or no effect on the condition of mussels. In all cases encountered by us, the magnitude of effects due to variations in host length, stage of gonad development, seasonal cycles and environmental factors, including thermal and starvation stress, is much greater than that due to parasitism. Thus from the biological point of view there is no reason why mussels in heavily infested areas should not be exploited commercially but if mussels are artificially cultivated in such areas this should be done in situations which keep infestations to their lowest levels e.g. rope or raised stake cultivation in areas of maximum current speed (Hepper, 1955).

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Short Notes

The occurrence of the sand eel (*Ammodytes dubius*) in 0·1 m² van Veen grab samples taken during winter in Godhavn Havn, Disko Bugt

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An investigation of the marine benthos in selected localities near the Arctic Station, University of Copenhagen, at Godhavn, West Greenland (Curtis 1977; Petersen 1977, in press; Theisen 1973) yielded eleven specimens of the sand eel *Ammodytes dubius* Reinhardt, 1838. Although a total of 271 samples from 3 to 110 m were taken the sand eel was present in only 10 of these, all of which were taken during the winter and at shallow depths (3–7 m). This material throws light on the life history of the sand eel in Disko Bugt (see also Holmquist, 1958). Most of the specimens were taken through holes in the sea ice. Ten of the sand eels were caught in the shallow part of the locality Godhavn Havn (69°15′N, 53°34′W). The results are summarised in Table 1 which also gives the length in mm of each of the sand eels. Godhavn Havn is an exposed marine locality with sand, pebbles and rocks. In a sheltered brackish-water locality (Fangsthytten) only a single sand eel, 70 mm long, was caught, at 10 m depth, through an icehole (11 March 1959). Sand eels were not caught in any of the grab and dredge samples from deeper localities.

The material confirms the conclusion from the literature that sand eels in the northwest Atlantic are difficult to identify to species (see Jensen, 1941; Leim and Scott, 1966; Richards et al, 1963). The number of vertebrae in the present material ranges from 67 to 73, with 69 as modal value. The name *Ammodytes dubius* Reinhardt, 1838, seems most appropriate in all respects.

The grab samples suggest that in the Disko Bugt area sand eels apparently hibernate, buried in the sediment at shallow depths, from late November until May. The temperature at the bottom during this period is about −1·7°C, and there is practically no light. The polar night starts in the first week of December, and a layer of sea ice about 1 m thick covers the area until late May (Petersen, 1964; Figs 4 and 12). The density of sand eels is about 3–6/m² in the shallow sand bottom. The material seems to consist of two size groups: one of 60–96 mm and another of 123–143 mm.

K. Popp Madsen (The Danish Institute for Fishery and Marine Research) has informed me, that from

Table 1. Depths of 93 bottom samples taken by 0·1 m² van Veen grab in Godhavn 1958–1959. The number of grab samples and length of sand eels (*Ammodytes dubius*) taken are given. *n* = number of grab samples; *l* = length in mm of sand eels. Sea ice was present in March and April.

Depth in m	March		April		June		August		September		October		November	
	n	*l*	*n*	*l*	*n*	*l*	*n*	*l*	*n*	*l*	*n*	*l*	*n*	*l*
3	–	69	3	123, 129	–	–	–	–	–	–	–	–	1	69
4	2	95	11	140, 143	2	–	5	–	6	–	–	–	3	75
5	3	–	–	–	2	–	1	–	–	–	1	–	3	132
6	2	–	3	–	2	–	3	–	–	–	1	–	1	–
7	2	–	2	60	1	–	1	–	–	–	2	–	–	–
8	–	–	–	–	1	–	–	–	2	–	3	–	1	–
9	2	–	–	–	–	–	–	–	–	–	1	–	1	–
10	3	–	–	–	1	–	–	–	–	–	–	–	1	–
11	2	–	–	–	–	–	–	–	2	–	–	–	–	–
12	–	–	4	–	–	–	1	–	–	–	–	–	–	–
13	4	–	–	–	–	–	1	–	–	–	–	–	–	–

the data of the commercial fishery he estimated the density of sand eels on the North Sea fishing ground to be 13/m^2. Twenty-two van Veen grab samples yielded a total of 13 sand eels corresponding to a density of 2–4/m^2. He also informed me that during winter sand eels occur on tidal flats, buried deep in the substrate.

Comparing the observations from Disko with the above-mentioned results and the sand eel fishery in the North Sea, it is suggested that a large unexploited stock of sand eels might be found in Disko Bugt. Hitherto a small experimental sand eel fishery has only been carried out off Godthåb in 1969 (Bertelsen and Hansen 1970, p. 86). A sand eel fishery along the east coast of Disko with bottom trawl at 2–8 m depths might be remunerative in Disko Bugt during November. Here the bottom is suitable and the sand eel presumably hibernates in shoals and will probably stay buried during the days, which are very dark and short in November. The sea ice will prevent a fishery in December.

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The use of trawling in conjunction with plankton surveys as an aid to fish egg identification in the west central North Sea

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The eggs of cod (*Gadus morhua*) and those of haddock (*Melanogrammus aeglefinus*) cannot be distinguished until pigmentation has developed on the tail of the developing larva inside the egg (Russell, 1976). This has handicapped the description of cod and haddock spawning areas where both species occur together and, in particular, precludes the estimation of egg mortality rates.

Cod and haddock occur together off the northeast coast of England and, since both species are currently being studied by the Ministry of Agriculture, Fisheries and Food, it seemed useful to explore the extent to which cod and haddock eggs could be distinguished in plankton samples on the basis of a comparison of the distribution of eggs with the distribution of mature fish as shown by trawling.

The plankton and trawl surveys were carried out between 27 February and 7 March 1975 from RV "Corella". The plankton survey preceded the trawl survey and was completed on 2 March.

Plankton samples were collected using the 50 cm diameter version of the Lowestoft multipurpose high-speed plankton sampler (Beverton and Tungate, 1967) fitted with a 20·3 cm diameter nose-cone and a net of 23·6 meshes/cm (60 mpi). The sampler was towed at five knots in a "double oblique" haul (surface to bottom to surface) at each station of a regularly spaced grid of 38 stations. Fish eggs and larvae were staged, identified as far as possible and expressed as numbers/m^2 using the flowmeter readings and the calibration constant of the flowmeter calculated from hauls without the net. The stage

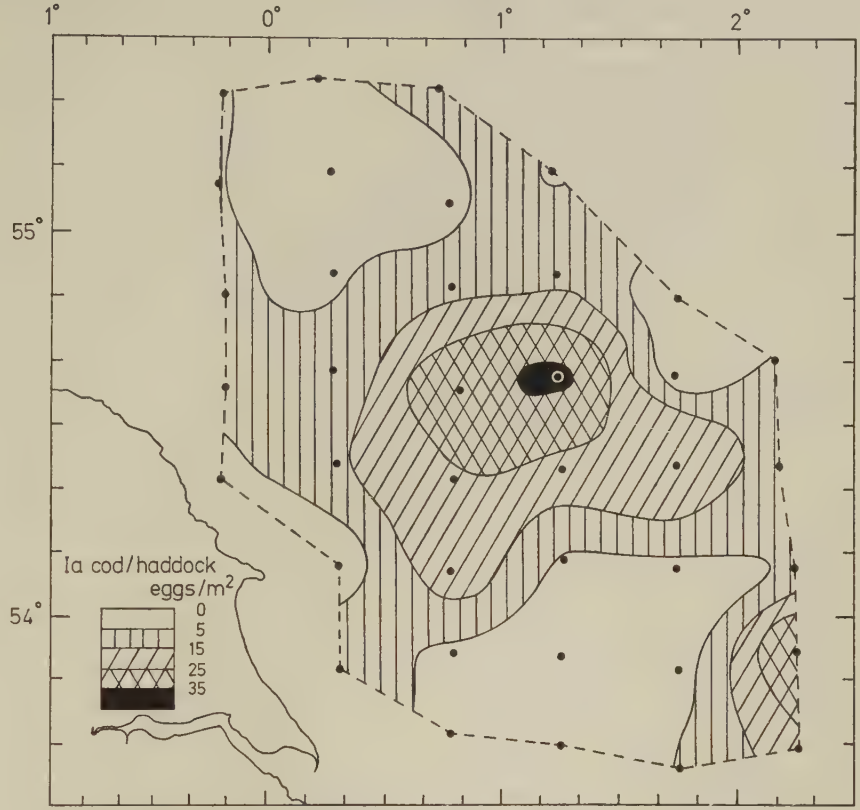

Figure 1. Distribution of stage 1a cod/haddock eggs between 27 February and 2 March 1975. Contours at 5, 15, 25 and 35 eggs/m^2 intervals.

criteria have been described by Harding et al (1974).

Trawling was carried out with a Granton otter trawl of 25 m headline length, fitted with 27·4 m bridles and 30·8 cm rubber bobbins on the footrope. The codend was 70 mm mesh size blinded with shrimp-netting of 19 mm mesh size. The trawl was fished for one hour at an average of 3·65 knots through the water and 3·09 knots over the ground at each of 20 stations within the area of the plankton grid. All cod and haddock were measured at each station and length stratified samples were examined for maturity stage. Estimates of the total number of mature fish were derived from these samples and expressed as number/hour of fishing.

Figure 1 shows the distribution of stage la cod/haddock eggs, which, at the prevailing sea surface temperature of 5·4 to 6·7°C, were between 1·2 and 1·4 days old. Figures 2a and b show the distributions of mature cod and mature haddock respectively, as shown by the trawl survey. It is clear that the distributions of mature cod and of eggs coincided and that the centre of each distribution occurred at 54°35′N 1°00′E. A second patch of cod/haddock eggs was identified in the southeast corner of the plankton grid at 53°50′N 2°15′W. Few mature haddock were caught within the 15 eggs/m^2 contour although high concentrations of mature haddock were found 35 km northeast and also 80 km northwest by west of the main centre of the stage 1a egg distribution. No haddock larvae or stage V haddock eggs were identified in any of the plankton samples although cod larvae and stage V cod eggs were present.

Each trawl station was located within a square of four plankton stations. The mean number of stage 1a eggs/m^2 per square (y) was calculated using the following formula:

$$y = \exp\left[\frac{\Sigma \ln(l + y)}{n}\right] - 1$$

where y is the observed number of eggs/m^2 at a station and n is the number of stations per square. This procedure is equivalent to calculating the geometric mean of the observations and allows one to include observations with zero value. Figure 3 shows

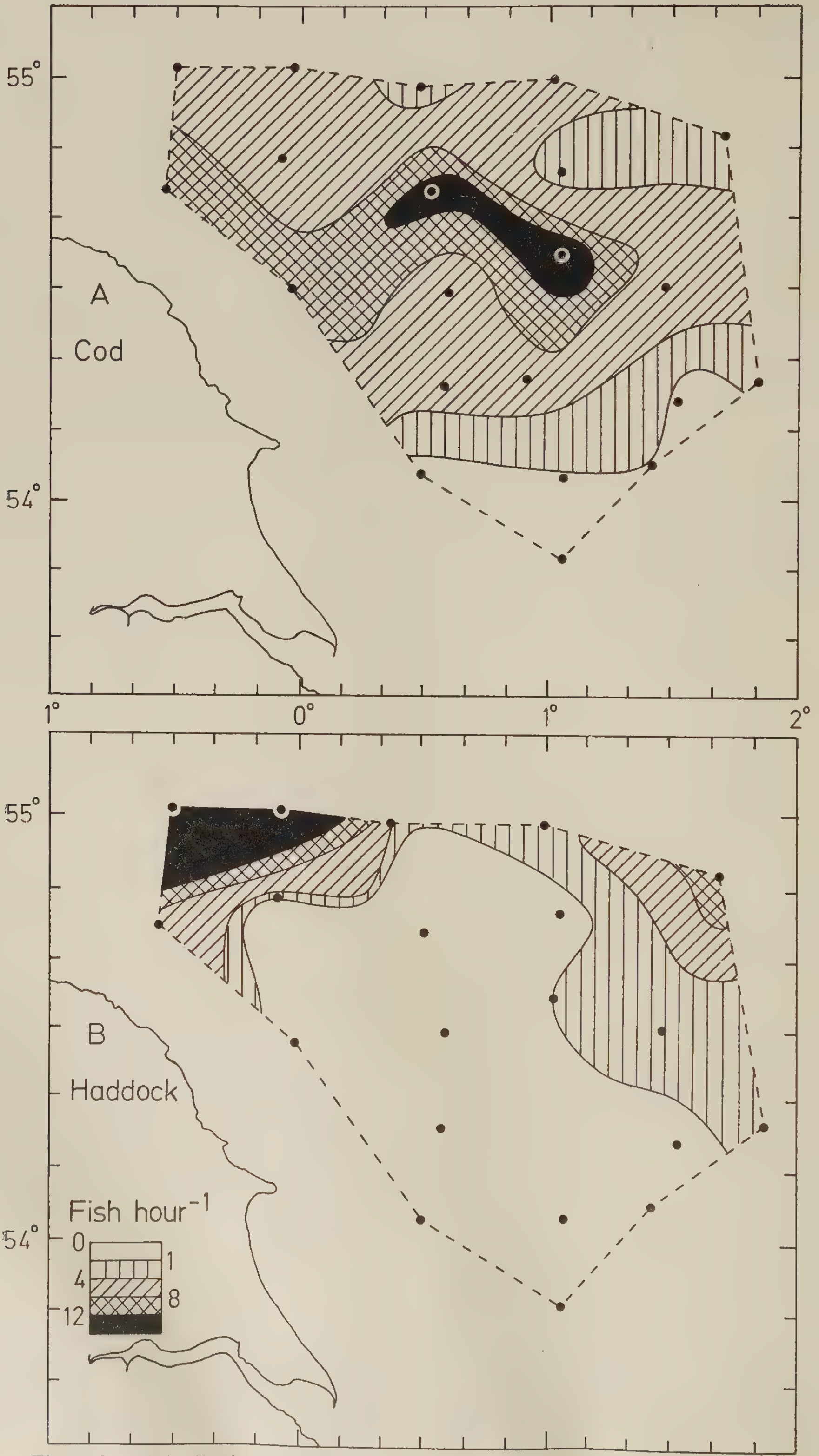
55°
54°
A
Cod
1°
0°
1°
2°
55°
B
Haddock
Fish hour⁻¹
0
1
4
8
12
54°

Figure 2. a. Distribution of mature cod between 2 and 7 March 1975. Contours at 1, 4, 8 and 12 fish per hour's fishing. b. Distribution of mature haddock between 2 and 7 March 1975. Contours at 1, 4, 8 and 12 fish per hour's fishing.

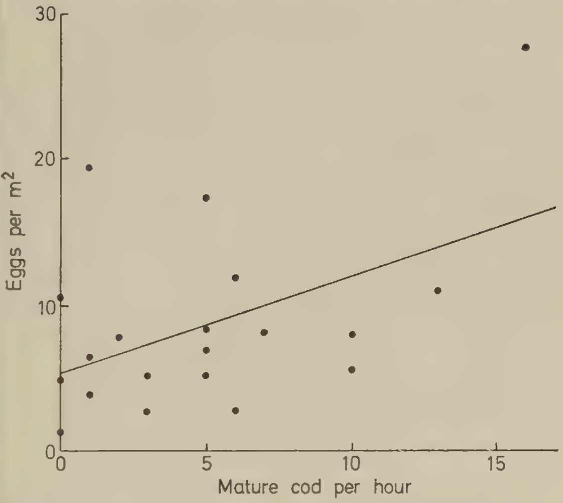

Figure 3. Relationship between the mean number of stage 1a cod/haddock eggs per m^2 and number of mature cod per hour's fishing. $r = 0{\cdot}47$ for 18 degrees of freedom, $P < 0{\cdot}05$.

the relationship between the mean number of eggs/m^2 and the number of mature cod. The correlation coefficient was significantly different from zero for cod ($r = 0{\cdot}47$, 18 d.f. $P < 0{\cdot}05$) but was not significantly different for haddock ($r = 0{\cdot}28$, 18 d.f., $P > 0{\cdot}1$).

Even though a clear correspondence between the distribution of mature cod and of stage 1a cod/haddock eggs was found, concentrations of mature haddock were found in sufficiently close proximity to suggest that the patch of eggs could, in fact, have been haddock eggs which had drifted at least 35 km southwest during the 1·2 to 1·4 days since they were fertilised or 80 km to the southeast by east (assuming the same rate of development as the cod). This explanation would require a rate of residual drift of 25 km/day whereas observations with moored current meters in the vicinity have shown a maximum drift in February and March 1971–74 of 15·90 km/day at JONSIS station 2 at 54°23′N 1°06′E (Ramster, personal communication).

A further objection might be that the trawl survey took place between four and nine days after the time of fertilisation of the stage 1a eggs observed on the plankton survey and that the eggs were derived from a patch of mature cod or haddock not described by the trawl survey. The fact that later stage eggs and larvae of cod but not of haddock were found in the area of the patch of tage 1a eggs is evidence against the objection. It would, of course, have been desirable to have carried out the trawl survey before the plankton survey. If the technique is to be used routinely then this procedure would have to be followed as far as it is practicable to do so.

There is thus strong evidence that the patch of cod or haddock eggs found on the plankton survey was, in fact, a patch of cod eggs. The results confirms the notion, which was put forward by Graham (1923) on the basis of the presence of large cod in March, that cod spawn in the area off Flamborough. It is likely that the technique of trawling in conjunction with plankton surveys is a useful method of identifying fish eggs when it is not possible to distinguish them anatomically and when the spawning of the two species is to some extent separated spatially.

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Colour of the ocean as an indicator in photosynthetic studies

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Spectral analysis of the daylight backscattered from the sea yields information about the optical properties of the upper layer and ultimately about its content of suspended particles and coloured dissolved substances. Generally the spectral character of the colour of the upwelling light can be investigated by employing a two channel system. Thus a colour index is defined as the ratio of nadir radiance in the blue (450 nm) to that in the green (520 nm) (Jerlov, 1974).

$$F = \frac{L(180^\circ)_{450\,\mathrm{nm}}}{L(180^\circ)_{520\,\mathrm{nm}}}$$

This index is determined below the sea surface which avoids several severe complications — appearing in remote spectroscopy – due to reflexion at the sea surface, air light etc. (Clarke and Ewing, 1974; Austin, 1974).

The colour meter which is a simple and cheap instrument, is suitable for routine work: it is lowered manually from shipboard preferably down to one metre. A measurement of the index is accomplished in a few minutes.

The index can readily be fitted into the pattern of optical properties. A clear association is indicated between colour index and depths at which the percentage of surface quanta irradiance (350–700 nm) is 10% (Jerlov, 1974). It seems, however, important to broaden the basis for this comparison by utilizing new experimental material in order to investigate the potentiality of using the colour index in photosynthetic studies.

Experimental material

Table 1 presents a survey of the oceanic stations where combined observations of colour index and quanta were made. A considerable number of data were collected under different weather conditions in August 1975 and March–June 1976 during the Fladen Ground expeditions at a central position of 59°N 0°30′E in the North Sea. The typical upwelling area off West Africa is represented by data obtained during two cruises 1972 and 1975 in February, March.

A few but significant observations originate from the Gibraltar region and the Drake Passage. The bluest water is encountered south of Sardinia.

Results and discussion

A condensation of all observations of colour index (F) and 10% quanta level (z_{10}) is shown in Figure 1. Tentatively a straight line is chosen as the best fit to the points. The depth interval for the 10% level is from 10 to 40 m. Extrapolation to the deepest level – found in the Sargasso Sea – would give a maximum colour index of 4·8.

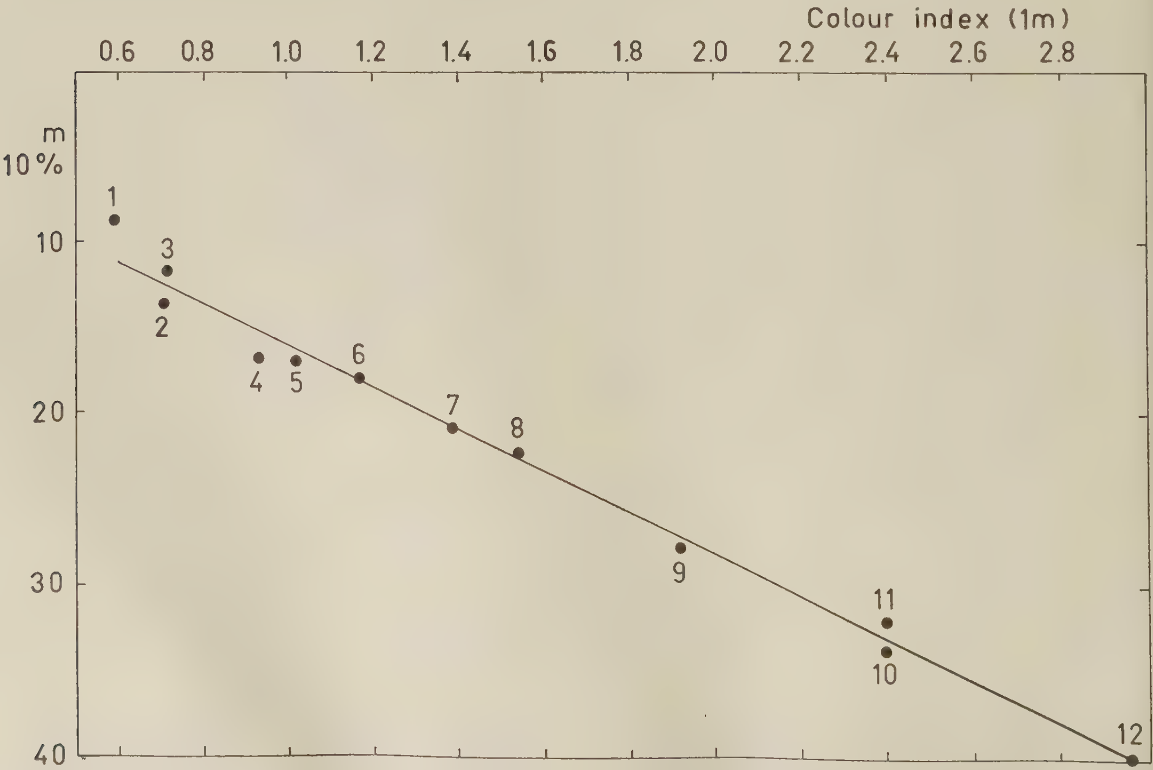

Figure 1. Relationship between colour index (1 m) and depth at which the percentage of surface irradiance of quanta (350–700 nm) is 10%.

Table 1. Oceanic stations where observations of the colour index and quanta measurements were made.

Notation	Region	No. of observations
1........	North Sea	28
2........	North Sea	18
3........	Off West Africa	9
4........	North Sea	18
5........	North Sea	23
6........	Gibraltar Strait	2
7........	North Sea	23
8........	North Sea	8
9........	East Gibraltar	1
10........	East Sardinia	2
11........	Drake Passage	2
12........	South Sardinia	5

Some considerations should be given to errors which generally occur in the measurements. The colour index can show variations within 10% due to cloud effects. On the other hand it is little dependent on solar elevation if above 15° (Jerlov, 1974; Højerslev, 1974a). On the contrary, the 10% level is influenced by the elevation. Experiments indicate a typical variation of ±10% for all atmospheric lighting conditions (Højerslev, 1974a; 1974b).

With overall decreasing quanta irradiance transmittance the shortwave part of the spectrum is reduced more than the longwave part because of selective absorption by particles and dissolved substances (yellow substance); accordingly the colour index also decreases. Chlorophyll has a specific effect on the index as it shows minimum absorption in the green and maximum in the violet.

With regard to possible errors in the mean values the scatter of points 2, 3 and 4 is not important. Only for point 1 does a real deviation from the straight line seem to occur. This deviation may probably be ascribed to the strong plankton bloom during part of the measuring period. With abundant living material daylight was much more scattered than absorbed: the content of yellow substance was relatively low as evident from beam transmittance measurements. On the whole the relation between the 10% level and the colour index becomes rather uncertain for indices below 0·6 and such values have, therefore, been omitted in Figure 1.

The close relation between index and 10% level is not immediately understood since the upwelling field can provide information only about the upper 20–25 m of clear ocean water (Gordon and Mc Cluney, 1975) while the 10% level is deeper. This level is chosen because it is in the middle of the euphotic zone and can be determined with adequate accuracy. In fact a recent investigation based on large material of quanta measurements in different water masses (Jerlov, 1977) shows the somewhat remarkable result that a constant relationship exists between different quanta percent levels. In essence this implies that oceanic waters can be classified in terms of transmittance of quanta irradiance for the whole euphotic zone.

The following conclusion emerges from the discussion: a simple and rapid determination of the colour index at one metre can be used to advantage instead of the more complicated quanta observation.

The index, if above 0·6, yields reasonably accurate information about the level of 10% quanta and ultimately about any other percent level in the euphotic zone (Table 2).

Table 2. Relation between colour index and different quanta percent levels

Colour index	Quanta percent levels (m) 30%	10%	3%	1%
0·6	5·4	11·3	18·5	24·5
0·7	5·9	12·5	20·5	27
0·8	6·5	13·6	22·5	29·5
0·9	7·0	14·8	24·5	32
1·0	7·6	16·0	26·5	35·0
1·1	8·1	17·2	28·5	37·5
1·2	8·6	18·4	30·5	40
1·3	9·1	19·6	32·5	42·5
1·4	9·6	20·8	34·5	45
1·5	10·0	22·0	36·5	47·5
1·6	10·5	23·2	38·5	50
1·7	11·0	24·4	40·5	52·5
1·8	11·5	25·6	42·5	55
1·9	12·0	26·8	44·5	57·5
2·0	12·4	28·1	46·5	60
2·1	12·9	29·3	48·5	62·5
2·2	13·4	30·5	50·5	65
2·3	13·8	31·7	52·5	67·5
2·4	14·2	32·9	54·5	70
2·5	14·6	34·1	56·5	73
2·6	15·0	35·3	58·5	75·5
2·7	15·4	36·5	60·5	78
2·8	15·8	37·8	62·5	80·5
2·9	16·2	39·0	64·5	83
3·0	16·6	40·2	66·5	85·5

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J. Cons. int. Explor. Mer, 37(3): 316–318

The responses of cod *Gadus morhua* (L) to chemical attractants in moving water

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Introduction

Cod can detect food by chemoreception (Pipping, 1926; Brawn, 1969), and are able to locate the source of attractive chemical stimuli in experimental tanks (McKenzie, 1935; Pawson, 1976). In these conditions the fish appear to detect chemical gradients and orientate by chemoklinotaxis or chemotropotaxis. Wild cod, however, inhabit tidal areas where their search for food on the sea-bed will be most efficient if they drift or swim with the current, and turn to swim upstream when chemical stimuli emanating from food are detected. This note describes an experiment designed to test the hypothesis that cod will show a positive rheotaxis in response to chemical attractants in moving water.

Materials and methods

The fish were required to swim with the current and not to hold station with the background, heading upstream, as often occurs with an optomotor response (Harden Jones, 1963). A perspex annular tank (274 cm in external diameter with a 30 cm trough containing water to a depth of 14 cm) was used to allow the fish to swim continuously in either direction, with or against a current produced by a Stuart-Turner No. 10 centrifugal pump. This was constant at 17 cm/s in the middle of the trough, as measured by timing a float. Although the water velocity could not be varied, its apparent velocity could be altered by varying the angular velocity of an irregularly striped black and white background on each side of the transparent trough. It was hoped that a velocity would be found at which the cod did not exhibit an optomotor response, but swam downstream. The apparatus was illuminated by a ring-shaped fluorescent tube and was surrounded by a blackout. The attractant (an aqueous filtrate of 5 g macerated frozen squid *Loligo* sp. mantle in 400 ml sea water) was introduced through a transparent 5 mm bore PVC pipe by gravity feed from a beaker. This was manipulated by the observer, who sat inside the annulus and recorded events with a Telford cine camera (8 frames/s), using a large circular mirror placed above the tank.

The swimming speeds of the fish were calculated by recording the time taken to swim between markers spaced round the tank. The sea water in the tank was changed after each test and remained between 10 and 11 °C throughout the experiment. Two 20 cm cod were used singly in order to observe their reaction to the moving background, and three more were used in the tests (two trials per fish) involving the chemical attractant. These observations were made at the Department of Agriculture and Fisheries for Scotland, Marine Laboratory, Aberdeen in April 1971.

Results

Throughout the trials to find a background speed at which the cod would swim with the current, the moving background did not appear to have any effect on their movements. They seldom swam more than half-way round the tank before turning and swimming in the opposite direction, and maintained the same speed relative to the tank in either direction. After these trials, however, the fish swam almost continuously downstream when the background was stationary! The following tests were carried out

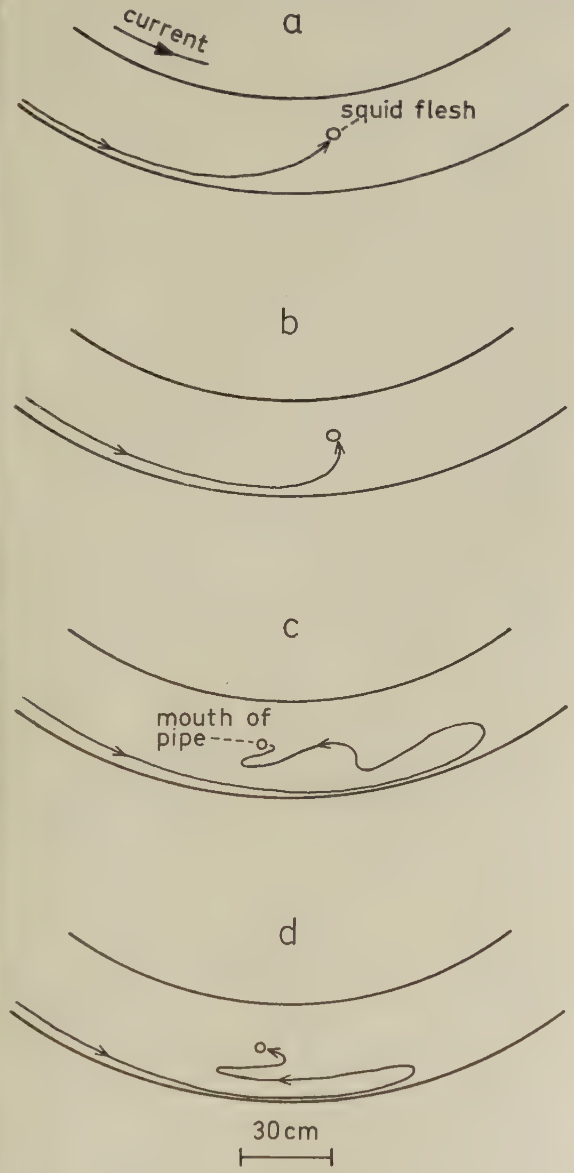
current
a
squid flesh
b
c
mouth of pipe
d
30cm

Figure 1. Tracks of 20 cm cod swimming with the current in the annular tank, when presented with a piece of squid flesh lying on the bottom (a and b), and with a colourless aqueous extract of squid flesh issuing from a pipe (c and d).

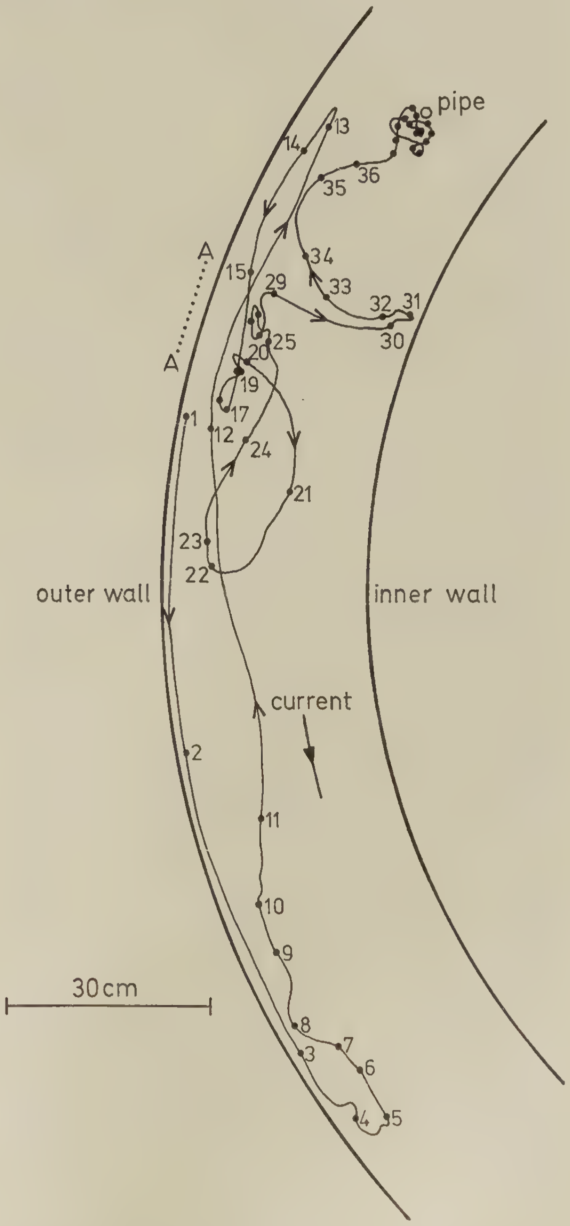
pipe
13
14
36
35
34
33
A
15
29
32
31
30
25
20
A
19
17
1
12
24
21
23
22
outer wall
inner wall
current
2
11
10
9
30cm
8
7
3
6
4
5

Figure 2. The filmed response of a cod to an extract of squid in moving water. Dots indicate positions of the fish's snout at 1 s intervals. Description in the text.

when the fish appeared to be settled and swimming steadily with the current.

When the pipe was present without a discharge of squid extract, it was always disregarded. However, if a piece of squid flesh was put on the tank bottom in place of the introduction pipe, to which it was visually similar, the fish appeared to see it whilst still upstream, and moved towards the centre of the trough to take the squid without going downstream of it. Figures 1 a and b, show the tracks (drawn by eye) of fish moving to take a piece of squid off the tank bottom. This indicates that in the course of the experiment the cod did not learn to visually associate the pipe with food.

The squid extract was introduced just behind and upstream of a fish, when it had swum undisturbed with the current four or five times round the tank. The flow of attractant was continuous for one minute. On passing the pipe during its next circuit the fish entered the chemical "corridor" between 50 and 200 cm below the introduction point, turned to face into the current, and then swam back towards the pipe, searching from side to side and occasionally darting forwards. If the pipe was passed the fish turned again and swam or drifted with the current until it re-entered the attractive area. The mouth of the pipe was usually located within 40 s of the fish first detecting the attractant, and was nudged and mouthed. Figures 1 c and d, show the tracks of two fish making this response.

A typical response of the cod to squid extract in moving water was filmed. This was examined frame by frame using a Specto Motion Picture Analyser and the fish's track plotted. This is shown in Figure 2, where the position of the cod's snout at intervals of 1 s after it passed the mouth of the introduction pipe are marked. After it had swum at 30 cm/s through the water to approximately 160 cm downstream of the pipe's mouth, the cod turned through 180° and swam slowly upstream (4–11 s), turning its head from side to side through an angle of about 20°. It then accelerated and swam near the outside wall of the trough at approximately 85 cm/s through the water for 1·5 s. When level with the mouth of the pipe the cod turned through 90° to face the outer wall of the through and drifted with the current for approximately 50 cm. The fish then turned to face upstream again (17 s) and after drifting for a further 40 cm it swam slowly upstream to area A ..... A. Here it lingered near the outside wall for 5 s, crossed to the inside wall (31 s), turned through 90° and returned to the outer wall above A ..... A. Still heading upstream the fish then swam towards the centre of the trough 25 cm above the point where it last crossed, and then to the introduction pipe's mouth. The cod stayed in the vicinity for at least 20 s, always heading upstream (±15°) and moving around the attractant source.

Discussion

The role of chemical attractants in food location by fish has usually been explained as a gradient effect, the recipient orientating by chemotaxis or chemokinesis to the stimulus source (Parker, 1914; Kleerekoper, 1967; and others). However, there is increasing evidence that the chemical stimulus may have an activating, and not necessarily a directional, effect, especially at a distance from its source. The above observations support the hypothesis that cod swimming with the current will turn and swim upstream on detecting an attractive chemical stimulus. This behaviour appeared to be a positive rheotaxis elicited by a chemical stimulus, and the subsequent rapid swimming against the current was probably an orthokinetic component superimposed on the rheotaxis. When the filmed fish swam upstream of A ..... A it presumably left the attractant "corridor", and it was observed to stop swimming and to drift with the current until it again encountered the chemical stimulus. In the region A ..... A the chemical gradients were probably sufficiently steep to allow a chemotaxis, and the cod soon localised the source of the attractant.

Similar observations of chemical stimuli which act as a sign stimulus releasing a rheotactic response in fish have been described for eels (Creutzberg, 1961), sharks (Hodgson and Mathewson, 1971) and salmonids (discussed in Harden Jones, 1968, pp 259–270). There is some evidence (Pawson; Harden Jones, unpublished data) that wild gadoids move with the current over the sea bed, and this mechanism offers search and energy advantages, particularly in strongly tidal areas and where visual food location is restricted.

Acknowledgements

I wish to thank Dr C. C. Hemmings for his help in carrying out this experiment. This research was part of a PhD thesis supported by the Natural Environment Research Council.

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Reviews

C. B. Officer: *The physical oceanography of estuaries.* John Wiley (Interscience). 1976. 465 pp. £ 19.75.

This book sets out to develop in detail the theory of tidal motion, circulation and mixing for estuaries and then to present examples of applications of the theory in a variety of estuaries distributed worldwide. A little over half the book is devoted to the first of these objectives; the first 96 pages give the fundamental hydrodynamics and tidal theory, including a useful introduction to bottom friction and the thin bottom layer shear zone. However, the repeated statement that above this layer the water velocity may often be taken as constant may mislead some readers. The effect of turbulence is considered early in the book and at this point little regard is paid to the limitations imposed by boundaries, some of the material being more applicable to the open sea than to estuaries. Turbulence spectra and the 4/3 power law for diffusion are discussed, but without illustrating their application in practice. Indeed, readers who use the book as an introduction to the subject would appreciate more references in the theoretical chapters to the situation found in various estuaries. For example, when discussing standing tidal waves, the likely magnitude of the wavelength is not quoted and no reference is made to estuaries mentioned in the second part of the book where such waves occur. Fifty eight pages are devoted to the theory of circulation in estuaries and much reference is made to the work of Stommel and Farmer in 1952 on stratified flows. Perhaps a little surprisingly discussion is included of the Ekman spiral, although no example is given of its practical importance in estuaries.

A chapter of 71 pages is devoted to mixing. The earlier discussion of turbulent diffusion might perhaps have been better included in this section, where it would have been easier to compare its importance with shear diffusion. The theory using segmentation proposed by Ketchum in 1951 is described in some detail. Consideration of vertical mixing is followed by discussion of the seasonal thermocline and heat effects, and here the author fails to resist the temptation to introduce material mainly relevant to the deep ocean, even reproducing diagrams showing the thermocline near Bermuda. The first part of the book is completed by a chapter on pollutant dispersal, and a quotation (p. 237) from this reveals one of the book's self-imposed limitations:

"For the dispersion of a pollutant there are two additional variables we must consider in addition to those normally considered in an investigation of an estuarine or coastal water body. These are the geometry of the coastal water body and the temporal and physical characteristics of the source itself ..... As regards the geometry the three dimensional bottom contour configuration of any given coastal water body usually does not lend itself to analytic description, let alone the inclusion of such a description in the defining equations." After considering briefly the difficulty of dealing analytically with the case of variable geometry it is concluded that: "Computer solutions in finite difference form appear to be a more satisfactory method of approach in such cases."

The second part of the book contains many examples quoted from published work on estuaries throughout the world. The intention in these chapters is to give the reader a sense of what the physical variation may be, the experimental and analytic techniques that have been used and the results obtained. Essentially this is a review section, as exemplified by the fact that of 140 diagrams only 3 are originals. In connection with results reported for the Severn and other estuaries there is some discussion of the process of flocculation. Some indication of the geographical location of the many estuaries mentioned would have been helpful, especially since the Fal and Blackwater appear with European coastal waters rather than British estuaries. In view of the obvious need to be selective in compiling such a book, it is surprising to find maps of the rainfall over Australia and a discussion of the work done on the moon by the tides of the Irish Sea. The book does not claim to include a discussion of modelling, but a few references to this are made, although Leendertse's detailed work in Jamaica Bay is not mentioned.

This book is most suitable for those who wish to acquire a fundamental knowledge of estuarine hydrography and an introduction to the wide variety of conditions encountered. In the main, it achieves what it sets out to do, providing a reasonably complete discussion of the fundamental theory of estuaries and giving a wide range of examples of published work. Those involved in detailed investigations of estuaries will find it a useful reference book; an extensive bibliography is included, much of it covering work of some years' standing. Indexing of references and authors is commendable. Throughout the book, emphasis is on fundamentals rather than the latest trend of research. The book is longer and covers a wider field than K. R. Dyer's "*Estuaries: A Physical Introduction*", (published in 1973 by John Wiley) which may be preferred by those who seek a more concise treatment.

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U.S. Dept. of Commerce, 1976. *Computer Programs in Marine Science*, N.O.A.A. Environmental Data Service, key to Oceanographic Records Documentation No. 5, U.S. Govt Printing Office, Washington D.C. 20402, 225 pp, U.S. $ 3.50

Computer programming consumes a large portion of resources within the marine science community. Much of this effort duplicates work which has already been done by others within the community. This publication was designed to reduce this waste by providing an indexed catalog of software that a programmer could use to find a pre-programmed solution to a current task. Each entry in the catalog contains a short description of the program, the language in which it was programmed, the machine on which it was designed to operate and a contact for obtaining the listing and/or deck.

On the surface this looks like a good solution to a real problem. However, this is not the case in actual practice. I have checked with the authors of about twenty programs listed in the "available from the originator only" group and almost universally find that they have not been contacted for their programs. Similarly, I have queried the programming community and found a similar indifferent attitude towards this type of catalog. Objections range from "It takes too long to obtain a copy – I need it today," to "I don't really know what I am getting as to documentation, program reliability, etc.". As far as I can determine, this publication and its predecessors have not been used extensively by the community.

There is obviously a need for such an index, but this one is not filling the need. The fault probably lies with both the designers and the users. It has been my observation that users would rather do it themselves than spend the time to look up a program, obtain the listing or deck, determine if the program really fits their needs, modify it, debug it, and test it to make sure it really fits their needs. This is not a unique feeling since I find similar responses in other fields where exchange of software has been attempted.

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A. W. Reed, Ocean Waste Disposal Practice, Noyes Data Corporation, Park Ridge, New Jersey, 1975, 336 pp, U.S. $ 24.00

In spite of its title the book deals in fact with only one type of ocean disposal of wastes, that is, dumping. It is compiled from a series of government sponsored reports, and its main purpose is stated to be the provision of scientific findings, evaluations and conclusions in relation to possible long term effects of pollution and man-induced changes to marine ecosystems. As would be expected there are very few clear-cut conclusions on either of these issues.

There are seven chapters covering the case for ocean dumping, defining wastes and their effects, parameters required for an assessment of the impact of ocean disposal, monitoring requirements, economic aspects and case studies.

The book is not particularly readable, but it is a very useful compendium of information and data not otherwise readily accessible. There are interesting revelations on past and present US dumping practices, for example disposal of waste insecticides and chemical warfare agents by dumping, and the disposal at sea of nuclear warship wastes either directly from the nuclear powered vessel in question or from support ships: practices which would now either be prohibited or require rather stringent control under the London Dumping Convention!

The scale of the dumping problem in coastal waters, as distinct from the river and pipeline input, is rather overestimated, and the chapter dealing with collection of relevant information for environmental impact assessment is exhaustive rather than practical. One is left feeling that insistence on such detailed assessment will make ocean dumping prohibitive on cost grounds, and perhaps result in the transference of pollution problems to other sectors of the environment.

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E. D. Goldberg (Ed.): *Strategies for marine pollution monitoring*. John Wiley (Interscience), New York and London, 1976. 310 pp, £ 12.90.

The title of this latest offering from the Ed Goldberg stable is a little misleading. Both the title and the dust cover fly-sheet would have the reader believe that the book tackles topics such as the need for marine pollution monitoring, what should be measured, how, and on what sort of samples. It does not really do this, although it does discuss in some detail what samples can be taken and which pollutants can be measured and how. This is unfortunate, as a further look inside reveals that Professor Goldberg has persuaded many eminent marine scientists to join him in this venture and the product is of as high a standard as one might expect from such authors.

The book is divided into four parts of which the first two deal with analytical methods for organic and inorganic species respectively. The third deals with what are described as "analytical aids" but which might more accurately be described as general analytical techniques, precautions and requirements. The concluding section deals with sampling sites and materials and how to assess transport paths. Each chapter has been written by a different author or group of co-authors, and this has resulted in a considerable difference in format between the chapters. This is particularly noticeable in the sections on techniques where the approach adopted ranges from a review-type chapter, with illustrative examples, on petroleum hydrocarbon analysis, to an analytical method type of approach in the chapter on phthalates.

Although this difference in format is distracting, each approach is effective in its own way. The different chapters on methods of analysis cover petroleum hydrocarbons, polychlorobiphenyls and DDT compounds, low molecular weight halocarbons, phthalates, plastics, pelagic tar and litter, metals (by neutron activation analysis and atomic absorption spectroscopy) and plutonium. Each should prove very useful, both to those starting in the field of marine monitoring and those who are already involved, but wish to extend their range of coverage. Inevitably the different authors have assumed different levels of expertise in their readers and this is a pity. In a book of this type it is really safest to explain why certain precautions need to be taken, why certain apparatus and steps are required etc. Some authors do this admirably, others do so partially and others hardly at all.

It would be surprising if one could seriously fault the methodology sections but there are minor points of criticism especially in relation to the chapters on polychlorinated biphenyls and DDT and that on AAS methods for metals; some of the methods proposed here are unnecessarily time-consuming and complex, and recent work would suggest that the method for arsenic estimation is likely (in organisms at least) to provide an underestimate of the true value. It is also worth noting that the method proposed for pelagic tar makes no mention of that at present in use in the IGOSS Pilot Project on Monitoring involving petroleum.

In the section on "analytical aids" there is a useful chapter on separation and concentration of seawater constituents by synthetic ion exchange resins which lists techniques for a wide range of elements. There are two short chapters on intercalibration which could usefully have been combined. The one dealing with the formulation of reference materials relates principally to lead which is now recognised as one of the most complex analytical problems faced by the modern day analyst due to the immense problems of contamination, and the other briefly describes what reference materials are available from the National Bureau of Standards. By combining these two rather specialised chapters a little more could have been made of this very important topic and it could have been given a slightly more general flavour. To some extent however this is compensated by the individual chapters on pollutant categories, where in most cases reference is made to the need for intercalibration and the availability of suitable reference materials. The third section also includes a chapter which perpetuates the misleading nature of the book's title. The chapter is entitled "aids to analysis of sea water" but fortunately goes on to cover other types of marine samples, including sediments and organisms. Although both are orientated towards the needs of a United States monitoring scheme, and the stations and species are specified accordingly, it is fair to say that in almost all cases the reasons for the choices are clearly specified. The reasoning provided is in fact clear enough to be of far wider value than the actual sites etc. might perhaps indicate.

If the results of any monitoring programme are going to be interpreted and used to judge what is happening in the environment it is essential that the inputs of the pollutants be carefully assessed. There is an excellent chapter dealing with this topic. Each of the major pathways is described and the relative importance of different pollutants is discussed. As with the previous two chapters the conclusions relate to a programme for a US study, but the reasoning should be readily capable of application to other areas. The necessary precautions for sampling are given for each pathway and, where particular procedures etc. are recommended, the reasons are clearly spelt out.

At £ 12.90 a copy, the book is not expensive by present day standards and should be worth that amount to the readership it addresses. In spite of the "separate author" approach there is little repetition and there is a comprehensive and apparently accurate index. Where repetition does occur this is probably essential. Thus each chapter on methods assumes that, for example, someone interested in PCB analysis will not read that on metals and each has its own section on sampling precautions, contamination, and intercalibration needed to ensure precision and accuracy. In short a valuable addition to the field of marine monitoring literature, provided one is not misled by the title.

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